The marine red algae of Natal, South Africa: Order Gelidiales (Rhodophyta)

Richard E. Norris

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THE MARINE RED ALGAE OF NATAL, SOUTH AFRICA: ORDER GELIDIALES (RHODOPHYTA)

by

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Cover: *Ptilophora pinnatifida*, a relatively common species, mostly subtidal, on Natal's south coast. Drawing by O. Anderson.

Contents

Abstract

NORRIS, R.E. 1992. The marine red algae of Natal, South Africa: Order Gelidiales (Rhodophyta). *Memoirs of the Botanical Survey of South Africa* No. 61, pp. 43.

Natal, South Africa, includes a small northern region of tropical marine flora and extends through subtropical types to warm temperate in the south. Red algae are abundant in subtidal and intertidal habitats along this coast and this report is the first in a series on the benthic marine red algae of Natal. The Rhodophyta are reviewed and higher taxa are described, including a key to the orders of Florideophycideae occurring in Natal. The Gelidiales contain some of the largest and more common species of red algae in Natal. Twenty species are included in this report including eight species of *Gelidium* Lamouroux, two species of *Onikusa* Akatsuka, seven species of *Ptilophora* Kützing and three species of *Gelidiella* Feldmann & Hamel. *Pterocladia* J. Agardh is not recognized as a genus separate from *Gelidium*.

Uittreksel

Natal, Suid-Afrika, sluit 'n klein noordelike streek van tropiese seeflora in en strek deur subtropiese tot warm gematigde tipes in die suide. Rooialge is volop in subgety- en tussengetyhabitats langs hierdie kus. Hierdie verslag is die eerste in 'n reeks oor die bentiese seewater-rooialge van Natal. 'n Oorsig van die Rhodophyta word gegee, hoër taksons word beskryf en 'n sleutel tot die ordes van Florideophycideae wat in Natal voorkom, word verskaf. Die Gelidiales bevat sommige van die grootste en meer algemene spesies rooialge in Natal. Twintig spesies word in hierdie verslag ingesluit: agt van die genus *Gelidium* Lamouroux, twee van *Onikusa* Akatsuka, sewe van *Ptilophora* Kützing en drie van *Gelidiella* Feldmann & Hamel. *Pterocladia* J. Agardh word nie afsonderlik van *Gelidium* erken nie.

Introduction

This, the first in a series of publications reviewing the marine red algal flora on the coast of Natal, South Africa, covers a region extending from the Mozambique border in the north, a tropical marine environment on the southern edge of live coral reefs in the southwestern Indian Ocean, to the southern border of Natal, which is a warm temperate marine habitat. Red algae in Natal are more abundant than other kinds, but individual plants are often smaller than the other two main components of the benthic marine algal flora, the green and brown algae. There have been relatively few publications on the marine benthic algae of Natal, but a list of species from Inhaca Island, a region near the Natal northern border, was published (Pocock 1958), as well as a list of algae from Maputaland by Seagrief (1980) and a list of South African marine algae by Seagrief (1984) including species from Natal. More recently Norris and colleagues have discovered new taxa and provided new records of red algae for this region in addition to structural, reproductive and taxonomic details on a variety of taxa (Norris 1985, 1986a–c, 1987a–j, 1988a–f, 1989, 1990a, b, 1991, 1992a–c; Norris & Aken 1985; Norris, Hommersand & Fredericq 1987; Norris & Molloy 1988; Norris & Wynne 1987; Gordon-Mills & Norris 1986; Wynne 1984; Wynne & Norris 1991).

Division Rhodophyta

The Rhodophyta is a plant division that is structurally diverse and often spectacular in form. Some types are extremely small, a few genera being unicellular or comprised of a few cells and visible only with the aid of higher magnification; most species, however, can be observed with relatively low power magnification or with the unaided eye.

Magne (1989) proposed a new system of classification for the Rhodophyta in which three subclasses were recognized on the basis of thallus form, presence or absence of connections between cells and the method of cyst (spore) formation. I believe in the merit of this scheme and have adopted the general hypothesis proposed by Magne. Instead of recognizing Magne's main categories at the level of subclass, however, I prefer to elevate them to class status:

Class Archeorhodophyceae *(Magne) R.E. Norris*, stat. nov.

Archaeorhodophycidae Magne, Cryptogamie-Algologie 10: 112 (1989).

Red algae with unicellular or pseudofilamentous structure, reproduction by cell division and without transformation of fertile cells into cysts (including the Porphyridiales).

Class Metarhodophyceae *(Magne) R.E. Norris*, stat. nov.

Metarhodophycidae Magne, Cryptogamie-Algologie 10: 112 (1989).

Metacysts produced in which part of a parent cell is converted into a single fertile cell (including the Erythropeltidales, Rhodochaetales and Compsopogonales).

Class Eurhodophyceae *(Magne) R.E. Norris*, stat. nov.

Eurhodophycidae Magne, Cryptogamie-Algologie 10: 112 (1989).

The entire contents of a parent cell are converted into a single or several fertile cells. The often recognized subclasses, Bangiophycidae and Florideophycidae, are inserted into the Eurhodophyceae.

The Bangiophycidae have cytological, structural and reproductive characters that are very different from the Florideophycidae, the details of which will be explained more fully in a future section of the Natal red algal flora.

Subclass Florideophycidae

Most red algae are florideophytes, all of which are multicellular and have a wide range of thallus structure. Thalli may be prostrate filaments or crusts, separate erect uniseriate filaments, multiseriate filaments, or congenitally united filaments forming plants with uniaxial or multiaxial growth and producing cylindrical to flattened thalli or foliose blades. Most thalli are derived from apical growth.

It is important to emphasize the fact that Florideophycidae thalli, unlike the Bangiophycidae, are comprised of cells arranged in filaments which may remain free from one another or become congenitally fused into large fleshy or cartilaginous thalli. The filamentous structure may become obscured in the latter types. The tissue of some thicker species is comprised of enlarged cells resembling parenchyma, but early stages of development reveal a basic cell arrangement in filaments and the tissue is therefore a pseudoparenchyma. All Florideophycidae have initial development through the activity of a single apical cell (uniaxial) or a group of apical cells (multiaxial). A few types have growth in proximal regions of thalli (Norris & Kim 1972). Cells in filaments are attached to one another by primary pit connections (also termed pit plugs because electron microscopy shows no protoplasmic continuity

between adjacent cells), and secondary pit connections are formed in many species, even some that are uniseriate filaments. Pit connection cap layers, observed in ultra-thin sectioning for electron microscopy, characterize certain groups of red algae (Peuschel 1989). Cells are uninucleate or multinucleate, varying in cell types within the same thallus. Variations in this condition may also be characteristic of particular taxonomic groups.

External cells in thalli, or almost any cell that is exposed to considerable light, have one to several to many chloroplasts; pigments in the chroloplasts are varied, but chlorophyll *a* is always present as well as phycoerythrin and, in numerous species, phycocyanin. Phycoerythrin or both of the latter two accessory pigments dominate within the chloroplasts and give the many shades of red that may be found in species of Rhodophyta. With such varied coloured pigments, however, it is not surprising to find that red algae may also be shades of green, blue, brown or even blackish. Cell walls or spaces between them may accumulate substances peculiar to red algae such as agarose or carrageenan, and calcium carbonate in the form of calcite or aragonite may be deposited in some species or groups of species.

Sexual reproduction is common in the Florideophycidae and occurs without the benefit of flagellate cells. There is only heterogamy in the red algae, female and male reproductive organs sometimes occurring on the same plant. More often, however, plants are dioecious, and the gametophytes are often isomorphic. The male gamete (spermatium) is very small, colourless, and is released from a spermatangium, many of which occur in special capitulate clusters, sori or on the surface of branchlets. Carried by currents of water, spermatia attach to a receptive region of a protuberance (trichogyne) on the female gamete (carpogonium). Post-fertilization processes are complex in most species, usually involving transfer of the diploid nucleus, or one of its division products, to other cells within the female reproductive organs or cells remote from this structure. Divisions occur within and from the cell receiving the diploid nucleus producing an enlarged diploid tissue (gonimoblast tissue) that produces diploid spores (a single carpospore within each carposporangium) that are released from the female plant. Carpospores grow into diploid plants, the tetrasporophytes, that usually are isomorphic with gametophytes, but some species have heteromorphic tetrasporophytes and gametophytes. Tetrasporangia, the site of meiosis in the life history, occur within fertile areas of tetrasporophytes, occasionally a specialized organ, each producing four haploid spores, two growing into male plants and the other two into female plants. Arrangement of spores in the sporangia may be cruciate, tetrahedral or zonate.

Asexual propagation occurs in many species, sometimes by special propagules or spores (monospores, etc.) or by fragments of plants. Branches or even individual cells of many species can be used for their propagation. Many Florideophycidae have perennial thalli, survival through conditions unfavourable for growth often occurring by perennation of prostrate or holdfast parts of thalli. Other species may perennate through production of small filamentous or prostrate phases of the life history, often the tetrasporophyte, that may grow in rock fissures or other cryptic habitats.

Classification of Florideophycidae into orders and families is complex and often confusing, and has recently been reviewed by Garbary *et al.* (1982). Modern systems of classification are changing, particularly as our understanding of structure, the female reproductive system, post-fertilization stages and life histories is extended. At the present time the following orders are recognized in Natal: Acrochaetiales, Bonnemaisoniales, Ceramiales, Corallinales, Gelidiales, Gigartinales, Gracilariales, Hildenbrandiales, Nemaliales, Rhodymeniales. Characters of the female reproductive system are of primary importance in separating these orders, except for the Hildenbrandiales in which female gametophytes are unknown. Characters of female reproduction are often difficult to determine even when adequate female plant material is available. A key to these orders is provided, utilizing female reproductive characters, but with addition of more practical vegetative characters wherever possible.

Key to orders of Florideophycidae occurring in Natal

1a Thalli encrusting the substratum, comprised of closely adherent erect filaments without well-defined basal layers, without rhizoids; only tetrasporophytes known, tetrasporangia zonately divided, borne in conceptacles. Pit plugs with a single cap layer ..... Hildenbrandiales

1b Plants comprised of free uniseriate filaments or of uniseriate filaments having congenital fusions of walls forming solid, massive erect or encrusting thalli. Tetrasporangia cruciately, tetrahedrally or zonately divided. Gametophytes known for most species:

2a Carpogonium not on specialized branch or on 2–3(8)-celled branch of specialized cells; no special auxiliary cell present; carposporophyte developing from carpogonium or by fusion cell formed with carpogonium and various adjacent cells including the hypogenous cell:

3a Thallus comprised of uniseriate filaments mostly remaining free from one another; carpogonium distal or intercalary on otherwise undifferentiated branch, fertilized carpogonium directly producing the carposporophyte with few or no previous division or fusions with other cells. Pit plugs with two cap layers ..... Acrochaetiales

3b Thalli uniaxial or multiaxial, the main plant body not a uniseriate filament, but comprised of differentiated medulla and cortex; encrusting thalli having tissues oriented parallel or perpendicular to substratum:

4a Uniaxial thalli in which internal tissue is pseudoparenchymatous; elongate, unicellular thick-walled rhizines often present between large cells; carpogonia intercalary in third-order filaments from axial row in a distal furrow on branch, gonimoblast tissue developing from fertilized carpogonium, fusions of carpogonium with vegetative cells occurs; gonimoblast filaments fuse with specialized nutritive filaments in fertile region. Isomorphic phases in life histories. Pit plugs with a single cap layer ..... Gelidiales

4b Uniaxial or multiaxial thalli, cortex and medulla with pseudoparenchyma or comprised of narrow cells in filaments; carpogonial branch comprised of carpogonium plus 1–several nutritive rich or well-differentiated cells:

5a Uniaxial thalli with many regularly formed branches, outer cortex often thin, a mixture of large and small cells, sometimes with secretory (gland) cells; carpogonial branch 3-celled, on a multicellular apparatus of specialized cells; gonimoblast issues directly from carpogonium, or post-fertilization fusion of carpogonium with hypogynous cell occurs with resulting formation of gonimoblast filaments; carposporangia terminal. Some species isomorphic but heteromorphic life histories common with tetrasporophytes small and filamentous. Pit plugs without cap layers ..... Bonnemaisoniales

5b Multiaxial or uniaxial, cortex comprised of small-celled, often elongate filaments, medulla may be comprised of narrow-celled filaments or pseudoparenchymatous; thallus calcified or uncalcified:

6a Multiaxial, outer cortex usually compacted with large, colourless utricle cells and sometimes with small pigmented cells, both types may be present in some species; often calcified, medulla filamentous; isomorphic or heteromorphic life histories. Pit plugs with 2 cap layers ..... Nemaliales, Galaxauraceae

6b Multiaxial or uniaxial thalli having various forms, outer cortex usually of uniformly small cells terminating cortical filaments:

7a Multiaxial, usually mucilaginous thalli, some species containing granular or thin continuous calcification; medulla of periclinally arranged narrow-celled filaments, assimilatory filaments diverging along axis to form cortex which sometimes have terminal cells larger than interior ones; gonimoblast developing from fertilized carpogonium or it divides once, gonimoblast then developing from one or both products; often having heteromorphic life histories. Pit plugs with 2 cap layers ..... Nemaliales, Liagoraceae

7b Appearing to be multiaxial thalli, but early development is uniaxial, the axis rapidly becoming obscured; often cartilaginous, pseudoparenchymatous, small-celled cortex and medulla comprised of large cells. 2-celled carpogonial branches borne on intercalary supporting cell also bearing 2–several sterile branches; post-fertilization fusion of sterile branches onto carpogonium, resulting fusion cells developing multiple gonimoblast initials. Isomorphic life history. No cap layers in pit plugs .... Gracilariales

2b Carpogonial branch usually of 2–4 cells, (some genera having 8 or more cells), isolated laterally on vegetative filament or on a multicellular apparatus of specialized cells; post-fertilization utilization of auxiliary cells occurs in which they are present in the same system as carpogonial branch (procarp), or with an isolated vegetative cell serving as auxiliary cell, or the auxiliary cell is in a remote special cell system; auxiliary cells diploidized by outgrowths (diploid nucleated protuberances, cells or connecting filaments) from the fertilized carpogonium or carpogonial branch system:

8a Thalli uniaxial, some comprised of free uniseriate filaments, others with cortication directly adherent to and often matching the axial filament length (pericentral cells), sometimes with secondary cortication obscuring pericentral cells; diploidization of a cell (auxiliary cell) that is produced by the carpogonial branch system (procarpial) after fertilization. No cap layers in pit plugs ..... Ceramiales

8b Thalli multiaxial or uniaxial, uniaxial species not uniseriate; upright or encrusting; if encrusting, a well-defined basal layer of cells usually present:

9a Multiaxial thalli having dense continuous accumulation of calcium carbonate forming laminate crusts, upright thalli or segments of upright thalli; reproductive tissue restricted to conceptacles (encapsulated nemathecioid sori). Pit plugs with 2 cap layers ..... Corallinales

9b Uniaxial or multiaxial thalli with no accumulation of calcium carbonate, or granules of calcium carbonate may be present in less dense concentrations; not all or no reproductive tissue restricted to conceptacles:

10a Multiaxial encrusting or erect thalli with large-celled pseudoparenchyma in medulla; hollow or vesiculate thalli also common. Carpogonial branch 3–4-celled, on supporting cell also bearing pre-fertilization developed 2-celled auxiliary cell branch (procarpic). Isomorphic life histories. No cap layers in pit plugs ..... Rhodymeniales

10b Thalli erect or encrusting, erect thalli of greatly variable form and size, multiaxial or uniaxial and the medulla with narrow-celled filaments or large-celled pseudoparenchyma. Light granular calcification occurs in a few species. Cortical tissue usually comprised of branched chains of outwardly progressively smaller cells. Refractive secretory (gland) cells may occur in cortices of some species. Carpogonial branches secondarily formed, usually comprised of 3 cells but may be much longer, up to 24 in the Dumontiaceae (a family not found in Natal). Usually with a single carpogonial branch on each supporting cell but polycarpogonial species occur. Diploidization of auxiliary cells charcteristic, gonimoblast initiated in procarps or on auxiliary cells or the connecting filaments at places remote from the site of fertilization. Auxiliary cells cut off before fertilization in procarpial situations but may be formed after fertilization in non-procarpial types. Life histories isomorphic or heteromorphic. No cap layers in pit plugs. An order of convenience at the present time, almost certain to be split into several to many smaller orders, with greatly variable families, many of which have no close phylogenetic links to one another ..... Gigartinales

Order Gelidiales Kylin

Thalli saxicolous, on shells or epiphytic, usually much branched and cartilaginous, but a few species soft and fleshy; variously shaped, ranging from small cylindrical to flattened prostrate branches to erect branched or unbranched blades with membranous alae and midribs; colour highly variable, ranging from blackish to bright red to greenish brown; usually attached by a prostrate rhizomatous system of branches from which upright branches emerge; in smaller species prostrate system often indeterminate, producing determinate upright branches, but larger thalli usually have a determinate prostrate branching system producing a holdfast, and upright branches indeterminate.

Typical *Gelidium* species pinnately branched with a cartilaginous texture. Some species large, up to 0.5 m long, but other species very small, often a major component of algal turf. Prostrate branches usually dorsiventrally oriented, with attaching rhizoidal cells on proximal side that may be grouped together in peg-like attaching branchlets. Upright branches usually highly branched, lateral branches often emerging almost at right angles to axis. Growth is by means of an apical cell on each branch and the pattern of development of lateral branches may be very regular, often distichous. Cortex comprised of a few to several layers of cells, small outer ones gradually increasing in size inwardly. Young parts of thalli have a small-celled cortex and a large-celled medulla, all cells ellipsoidal to spheroidal.

Species in the Gelidiaceae produce *rhizines*, a characteristic type of filament in the internal tissues in which elongate unbranched cells have very thick walls leaving a lumen that is extremely small in comparison. Rhizines are produced in maturing regions of the thalli as a secondary tissue and they intrude between cells of the inner cortex and medulla. In some species the rhizines form distinct clusters within the inner cortex and may form the major part of the medulla. Other species may have rhizines only in inner cortical regions and the medulla may be secondarily formed thin-walled elongate cells in filaments that are derived from the large primary cells that originally formed the medulla. Many species have rhizines irregularly placed in both medullary and cortical regions. Rhizines are characteristic of species in the Gelidiaceae; the only other red algal group forming them are some members of the Solieriaceae. They are not present in the Gelidiellaceae.

Reproduction: tetrasporangial and gametangial thalli isomorphic. Reproductive structures located in mostly terminal sori, often on expanded branchlets. Tetrasporangia cruciately or tetrahedrally divided, formed by inner cortical cells and sunken within cortex. Spermatangia formed in large masses by outer cortical cells. Female reproductive cells produced in groups often centrally located in distal parts of branches. Carpogonial branches comprised of a single cell, the carpogonium, which is cut off in a regular intercalary position. After fertilization, vegetative cells in the filament that bears the carpogonium, produce special nutritive filaments, their cells having dense cytoplasmic contents. Fertilization also stimulates the production of a fusion cell between the carpogonium and the cell to which it is attached proximally (the supporting cell) as well as some of the adjacent vegetative cells. The fusion cell produces filaments that coalesce with nutritive cells and then produces gonimoblast filaments that form a tissue around the axis in the fertile area, eventually forming a swollen cystocarp with a cavity that has one to several ostioles opening into the spore chamber.

Despite the many carpogonial branches formed in groups on branch tips, usually only one cystocarp develops in a branch and it may have one or two locules. Ostioles usually are present, one produced for each locule. The only report of a female plant in the Gelidiellaceae is for an unknown species of *Gelidiella* by Sreenivasa Rao & Trivedi (1980). Additional details on carpogonial branch structure and post-fertilization stages are needed in order to assess relationships.

The combination of characteristics that unite the Gelidiales are the uniaxial thalli with single conspicuous apical cells present at the tips of each branch, only 2 periaxial cells produced on axial cells, a single cap layer in pit plugs (Peuschel 1989) and species are all agarophytes (the Graciliariaceae are also agarophytes). Possible phylogenetic relationships of the Gelidiales are proposed by Norris (1992a).

Characters of the female reproductive system in the Gelidiaceae are the accumulation of carpogonia in fertile branch tips, the unique post-fertilization stages in which filaments grow directly from a fusion cell formed from vegetative cells and fertilized carpogonia, the filaments uniting with characteristic nutritive filaments issued from vegetative cells and producing the sporogonous tissue in the cystocarp.

The Gelidiales is sometimes recognized as a family of the Nemaliales but, because the latter is heterogenous and without a clear relationship with the Gelidiales in life histories as well as in post-fertilization stages, it is better to recognize the group as a separate order.

Key to families of Gelidiales

1a Thalli having a distinct medulla in which elongate cells, often with a narrow diameter, occur in filaments. Subapical cell forming two periaxial cells that are distichously arranged on subsequent axial cells. Second order cell rows in erect branches distichously arranged. Rhizines are present in the medulla, in the inner cortex or in both regions ..... Gelidiaceae
1b Medulla and inner cortical cells often having cells of similar size and shape, elongate pseudoparenchymatous cells. Subapical cell forming two periaxial cells decussately arranged on subsequent axial cells. A core of narrower pseudoparenchymatous cells sometimes present but rhizines are never produced ... Gelidiellaceae (p. 33)

Family Gelidiaceae Kützing

Thalli erect or prostrate, usually cartilaginous, some species with a membranous wing bordering a midrib and some with surface proliferations. Erect thalli attached by a rhizomatous holdfast; this system is usually highly and often regularly branched, each branch terminated by a conspicuous apical cell. Subapical cell forms two periaxial cells, opposite one another and distichously arranged on subsequent axial cells, from which additional tissues and branching patterns derive their orientation. Internal tissues comprised of elongate medullary cells arranged in filaments, shorter pseudoparenchymatous internal cortical cells that gradate to small, compactly arranged outer cortical cells. Inner cortical cells and/or outer medullary cells produce few to many rhizines that often form a conspicuous tissue in the thallus. Rhizine cells elongate, up to 1 mm long (or more?) very narrow with extremely thick walls and a very narrow lumen.

Reproduction: male and female reproductive cells as well as tetrasporangia borne in distal parts of thalli or on special lobes or branches of thalli. These structures are mostly alike in all the genera of the family. Cystocarps may be uniloculate and with several carposporangia in chains in some species, but most have biloculate cystocarps with carposporangia borne singly. Also, ostioles of cystocarps may be formed only on the loculate side of the thallus but in most species they are formed on both sides of a biloculate cystocarp. Spermatangia are cut off by transverse rather than oblique cell divisions.

Key to Natal genera of Gelidiaceae

1a Thalli without a midrib and usually cartilaginous rather than having any membranous parts; indeterminate branching marginal although sometimes adventitious and from the flat surface. Reproductive structures borne on distal parts of thalli or on special lobes or branches. Rhizines mostly in the medulla or inner cortex. Large spheroidal cells not forming an inner cortical layer. Cystocarps mostly biloculate, occasionally uniloculate, carposporangia produced singly on gonimoblast filaments but occasionally borne in chains of two ..... *Gelidium*
1b Thalli usually having a distinct midrib bordered by membranous alae or broad and leafy, if without a midrib; indeterminate branching from the midrib or margin of blade:
2a Thalli with small rhizomatous holdfast, not forming extensive colonies. Indeterminate branching mostly marginal, occasionally from midrib. Surface proliferations sometimes present. Reproductive structures borne on proliferating branches. Rhizines often present in a layer beneath the outer cortex and large cells are present in the inner cortex ..... *Ptilophora* (p. 23)
2b Thalli often having rhizomatous holdfasts and usually occurring in large colonies. Indeterminate branching ramisympodial, from midrib surface. Surface proliferations usually sparse or absent. Reproductive structures borne on proliferating branchlets or on main blade. Inner cortex not with large parenchymatous cells; rhizines usually restricted to the medulla ..... *Onikusa* (p. 19)

GELIDIUM

Gelidium *Lamouroux* nom. cons., in Annales du Muséum National d'Histoire Naturelle, Paris 20: 128 (1813). Type species: *G. corneum* (Hudson) Lamouroux.

Pterocladia J. Agardh: 482 (1852). Type species: *P. lucida* (R. Br.) J. Agardh. For further discussion see Norris (1992a).

Thalli perennial, attached by rhizomatous and stoloniferous branches that often form a turf. Upright branches cylindrical to compressed, usually branched. Thalli uniaxial, with a cortex of few to several layers of angular to ovoid cells and a medulla consisting of large elongate colourless cells. Rhizines arising secondarily from inner cortical cells, extend into inner cortical and medullary regions.

Reproduction: tetrasporangia borne in sori on branch apices or in marginal proliferations. Female and male reproductive organs produced in distal regions, often on special proliferations. Mature cystocarps have one or two locules, a single ostiole or one or, more rarely, several ostioles on each side. Carposporangia produced singly, occasionally occurring in short chains.

Many regions of the world have two types of *Gelidium* in their flora, those that are comparatively large, usually over 50–60 mm tall, and those that are small, less than 30–40 mm, often forming a turf. Several species in each category often seem to be present in subtropical to tropical locations, the larger species usually not being difficult to indentify. The small species, however, are confusing in the literature and they are often classified as *G. pusillum* and its varieties (Borgensen 1943; Dawson 1953, 1954; Taylor 1945, 1960; Jaasund 1976; Santelices 1977; Stewart & Norris 1981; Schnetter & Bula Meyer 1982; Lawson & John 1987). Egerod (1971) assigned all small forms to *G. pusillum* without designating varieties. A study of *G. pusillum* in its type locality, Great Britain, by Dixon & Irvine (1977) has shown that this species varies in its form according to seasons and tidal level. Simply stated, the small cylindrical branching form of *G. pusillum* in Great Britain occurs in the high intertidal region and is more prevalent in shorter day-length periods of the year. Broader forms, the *G. pulchellum* type, having highly branched axes that often are pinnate, occur in the lower tidal regions

and in seasons having longer day lengths. In warmer regions of the world in which true *G. pusillum* occurs, therefore, one would expect to find the *G. pulchellum* type, especially in regions with little tidal range. Because it is likely that *G. pusillum (sensu stricto)* may be much more limited in its distribution and have a structure far less variable than previously believed, it is difficult to attribute many of the small growth forms of *Gelidium* in tropical and subtropical regions to *G. pusillum*.

Fertile plants of *Gelidium pusillum* in Great Britain, its type locality, are uncommon according to Dixon & Irvine. Fertile specimens of small *Gelidium* plants, however, have been found in many of the warmer regions and this is true of the specimens in Natal. Several of the South African species have been isolated into unialgal culture where they have maintained their typical structure as found in field collections, and they have also become fertile under the culture conditions. Unlike the British plants of *G. pusillum*, therefore, the South African small species of *Gelidium* do not appear to be a reduced form of a species that is larger and more highly branched under more constant and beneficial growth conditions. For this reason I prefer to recognize the possibility that true *G. pusillum*, as it is known in its type locality, does not occur in South Africa. At the present time I doubt that the several varieties described for *G. pusillum* from widespread tropical and subtropical localities can be accepted, its main distribution probably being mostly in warm temperate regions.

There is need for additional research on an international level to sort out taxonomic problems of the numerous taxa of small-sized *Gelidium*, a study that should employ comparisons of isolated cultures from many different regions. Until such a study can be done I prefer to utilize the published taxonomic treatments that are available for the variety of small species reported from Natal and similar regions.

Kylin (1938) described three small species of *Gelidium* from intertidal regions of central Natal, all of which can be recognized in our collections. One of these species, *G. caespitosum*, has been found with cystocarps that are typical for *Pterocladia*, into which it was transferred (Norris 1987e). Reconsideration of characters separating *Pterocladia* from *Gelidium*, however, later influenced me to abandon *Pterocladia* as a separate genus (Norris 1992a). Other small species of *Gelidium* are added to the Natal flora and three large branched species are recognized, *G. capense* (Gmelin) Silva ex Silva *et al.* (1987), *G. pteridifolium* R.E. Norris, Hommersand & Fredericq (1987), and *G. abbottiorum* R.E. Norris (1990b). It is anticipated that future research on *Gelidium* in Natal will uncover additional species, particularly in the turf environment.

Key to Natal species of *Gelidium*

1a Mature erect branches longer than 60 mm:

6a Thallus axis rarely more than 1 mm in diameter, secondary branches often unbranched, branch diameter frequently more than 1 mm. Distal branching often unequal and bipartite. Tetrasporangial sorus branchlets long and slender (1 × 0.5 mm) and without an apical incision. Cystocarps without a sterile 'beak' or with one that is short and blunt ..... 1. *G. abbottiorum*

6b Thallus axis usually 1 mm or more in diameter. Secondary branches rarely unbranched, secondary and tertiary branches often oppositely pinnately branched. Intervals between branches in distal regions usually 1 mm or less. Most distal branching tripartite. Tetrasporangial sorus branchlets often inverted cordate but if elongate having an apical incision. Cystocarps having a long sterile pointed 'beak':

7a Lower axes having mostly entire margins, abcission of laterals not leaving short stubs. Lateral branches not geniculate, mostly at right angles with the axis in young growing regions as well as in mature areas. Ultimate branches rarely congested, usually forming clearly defined pinnae, 10 mm or more in length 7. *G. pteridifolium*

7b Lower axes often serrate or having stubs of old branches along the margins. Lateral branches often forming an ascending angle with the axis, especially noticeable in growing apices, usually approximately 45° and often geniculate. Pinnae on lateral branches often congested, usually less than 5 mm long ..... 5. *G. capense*

1b Mature erect branches mostly less than 30–60 mm long:

2a Prostrate branches cylindrical to compressed, upright branches compressed, paired or up to five at one node, usually borne together with rhizoidal clusters at regularly spaced intervals; upright branches usually simple but occasionally pinnately branched and attaching, thereby often becoming prostrate axes. Cystocarps uniloculate with one ostiole ..... 4. *G. caloglossoides*

2b Prostrate branches cylindrical or compressed, upright branches and rhizoidal clusters not always borne together:

3a Upright sterile branches cylindrical, unbranched or sparingly branched up to 60 mm long. Outer cortical cells up to 13 μm long in surface view. Fertile areas expanded, often spatulate and distal on the upright branches ..... 2. *G. arenarium*

3b Upright sterile branches flattened and blade-like:

4a Upright branches broad (1 mm or more in diameter), foliose, unbranched or lobed, older branches sometimes once or twice pinnately branched, usually less than 30 mm high. Prostrate axes cylindrical to compressed:

5a Upright branches distichously and 1–2(3) times pinnately branched. Pinnae often crowded on larger plants but sparse on small thalli. Distal umbellate branches not formed. Blades up to 2 mm in diameter, not flexuous. Outer cortical cells small, typically 3 × 8 μm. Thalli often forming turf with other species; dark purplish colour. Cystocarps have two locules and ostioles on opposite sides of the blade ..... 8. *G. reptans*

5b Upright branches ligulate, narrow their entire length (usually less than 1 mm broad). Sometimes bearing distal clusters of long branches closely spaced and appearing umbellate. Thalli once, sometimes twice, pinnately branched, flexuous, up to 30(40) mm high. Surface cortical cells up to 10 × 15 μm. Thalli a rich purplish red colour, usually saxicolous. Cystocarps uniloculate having a single ostiole, carposporangia in short chains ..... 3. *G. caespitosum*

4b Prostrate axes cylindrical, often developed by decumbent and attaching upright axes. Upright branches lanceolate, margins entire, up to 2 mm long, 500 μm broad, unbranched, usually borne singly along the prostrate axis, not always in conjunction with rhizoidal bundles ..... 6. *G. minusculum*

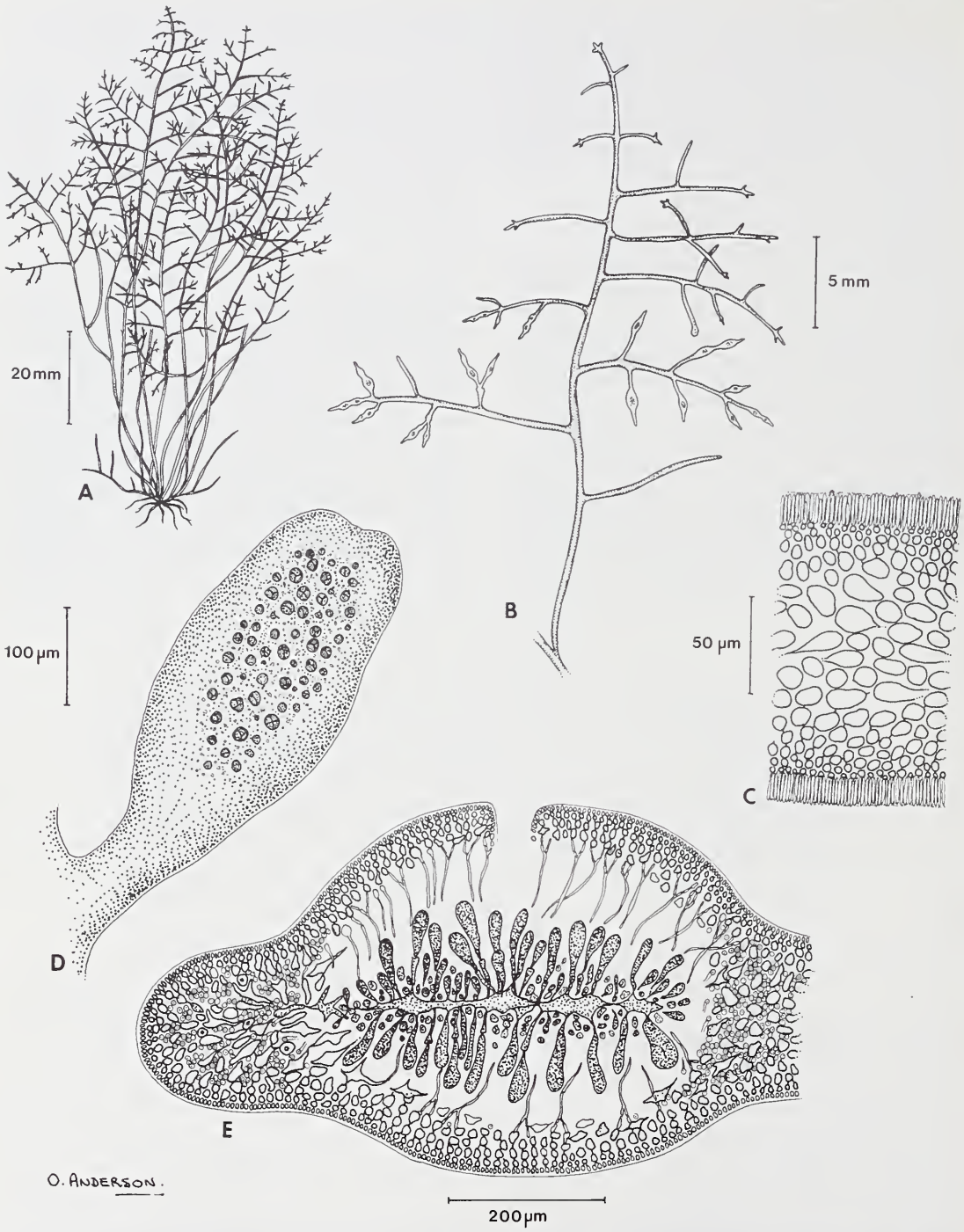

FIGURE 1.—*Gelidium abbottiorum*. A, habit of plant; B, enlarged cystocarpic branch; C, cross section of male fertile area; D, tetrasporangial bladelet; E, cross section of a cystocarp.

1. **Gelidium abbottiorum** *R.E. Norris* in Japanese Journal of Phycology (Sôrui): 41 (1990b). Type: Natal, Widenham, *Nat. 3768* (SAM, holo.!)

Gelidium amansii sensu Seagrief: 30 (1984); Norris *et al.*: 377 (1987).

Gelidium rigidum sensu Kützing: 16 (1868).

Icones: Kützing: t. 44d–g (1868); Norris *et al.*: 379, 380 (1987); Norris: 38 (1990b).

Thalli attached by a fibrous holdfast from which emerge many upright branches up to 200 mm in length (Figure 1A). Axes of upright branches up to 1 mm in diameter. Branches of axes often alternately arranged, unbranched or with only primary branches. Longer branches, especially if unbranched, often reflexed. Intervals between branchlets frequently more than 1 mm. Distal branches simple and narrow (up to 250 μm in diameter), branch tips often unequally bipartite (Figure 1A). Outer cortical cells up to 7.5 μm in diameter, but mostly much smaller; inner cortical cells ovate becoming angular and attached by long arms to cells of medulla, up to 25 μm in diameter. Medullary cells have thick walls, tissue appears webbed rather than parenchymatous because of long-armed cells. Rhizines located in small bundles in inner cortex, a few scattered in the medulla (Norris *et al.* 1987: fig. 11).

Reproduction: fertile branches often geniculate, terminal cystocarp or sorus directed distally (Figure 1B). Tetrasporangia occur in sori on ultimate lateral branches, which are up to 1.5 mm long, expanded soral area up to 500 μm in diameter (Figure 1D). Apical incision not visible under low magnification. Cystocarps occur in similar ultimate branchlets, usually near apex, may have a short sterile protuberance distally (Figure 1B), often absent. Cystocarps up to 0.5 mm in diameter, biloculate (Figure 1E). Male branchlets similar to tetrasporangiate, with a dense sorus of elongate spermatangial bearing cells without or with few intervening sterile cells (Figure 1C).

Distribution: South Africa (Natal, Transkei and eastern Cape).

NATAL.—2832 (Mtubatuba): Cape Vidal, on reef, female and tetrasporangiate, *Nat 2224*, 25-IX-1984, *NU 8102*; St Lucia, Mission Rocks, on reef, *R.H. Taylor 636*, 15-XII-1978, *NU 8516*; Mvoti River mouth, on reef, female and tetrasporangiate, *Nat 1669*, 17-III-1984, *NU 9043*. 2930 (Pietermaritzburg): Durban, Reunion Rocks, on reef, female and tetrasporangiate, *Nat 1831*, 16-IV-1984. 2931 (Stanger): Umdloti, on reef, tetrasporangiate, *Nat 1055*, 14-II-1983, *NU 7042*. 3030 (Port Shepstone): Park Rynie, Rocky Bay, on reef, female and tetrasporangiate, *Nat 2111*, 28-VIII-1984, *NU 9292*; Umdoni Park, on reef, *Jarman A17*, 12-X-1967, *NU 8515*. 3130 (Port Edward): Palm Beach, near Pt Edward, on reef, female, *Nat 1129*, 14-V-1983, *NU 7097*.

This is the most common large species of *Gelidium* in Natal, occurring intertidally, mostly in lower regions or tidal pools, its fibrous holdfast often forming a turf with adjacent plants. *G. abbottiorum* can be distinguished from *G. pteridifolium* by the narrower branches that are often more widely spaced; the tendency for ultimate branches to be unbranched and often reflexed unless they are fertile; and the sparse rhizines in the inner cortex. Large bundles of rhizines are also present in the inner cortex of *G. pteridifolium* as well as in the medulla of that species. The elongate tetrasporangial branches and the terminal or nearly terminal cystocarps on short branchlets in *G. abbottiorum* are also characteristics that may be used to separate it from *G. pteridifolium*. Fertile plants of *G. abbottiorum* often resemble *G. capense* but on a smaller scale and the distal fertile branches of *G. abbottiorum* are not so crowded on the axis as they are in *G. capense*.

2. **Gelidium arenarium** *Kylin* in Lunds Universitets Årsskrift, Ny Följd, Andra Afdelningen 34,8: 8 (1938). Type: Natal, Durban (Isipingo), *Kylin s.n.* (LD, lecto.!).

Icones: Kylin: 7 (1938). [Other published illustrations that are similar to this species: Kützing 1868, pl. 35a–c (as *Acrocarpus capitatus*); *Dawson* 1954, fig. 31e (as *Gelidium crinale* var. *perpusillum*); Coppejans 1983, pl. 300 (as *Gelidium ?pusillum–crinale?*)].

Thalli mostly of cylindrical prostrate branches, attached by bundles of rhizoids formed at regular to irregular intervals, forming upright cylindrical branches up to 30 mm high (Figure 2A, C). Branching irregular in both prostrate and upright systems, upright branches often remain unbranched. Prostrate and upright branches usually up to 250 μm in diameter. Surface cortical cells 7–13 μm in diameter, medullary cells up to 25 × 8 μm (Figure 2E). Rhizines, 3 μm in diameter, sparse, often occurring singly, mostly in medulla, concentrated in margins if thalli are compressed (Figure 2D).

Reproduction: tetrasporangial plants that were isolated into culture formed spatulate sori 1200 × 600 μm at tips of upright branches (Figure 2B). Sterile margin ± 75 μm wide surrounds sorus. Tetrasporangia spheroidal, up to 30 μm in diameter, separated by small outer cortical cells ± 3 μm in diameter. Gametophytes, developed in cultures but showing no signs of forming reproductive cells, have not been seen in field collected specimens.

Distribution: known only from Natal, from specimens grown in culture originally collected on a reef at Mvoti River mouth, a tetrasporophyte, *Nat 2449*, 16-III-1984. Gametophytes in culture have not developed recognizable reproductive structures.

Gelidium arenarium is similar to *G. crinale* but the thallus is smaller and rhizoidal clusters are usually formed in a fairly regular sequence on prostrate vegetative branches of *G. arenarium*. The larger size of the outer cortical cells in *G. arenarium*, compared with those of *G. crinale*, make it possible to separate sterile specimens of these two species. Also, the sparse rhizines in the medulla of *G. arenarium*, compared with the clusters present in inner cortical regions of *G. crinale*, may be useful in separating these species. *G. arenarium* is found in turf in central Natal but may be more widely distributed, its form being difficult to recognize from field collected specimens.

3. **Gelidium caespitosum** *Kylin* in Lunds Universitets Årsskrift, Ny Följd, Andra Afdelningen 34,8: 8 (1938). Type: Natal, Durban (Isipingo), *Kylin s.n.* (LD, lecto.).

Pterocladia caespitosa (Kylin) R.E. Norris: 42 (1987e).

Icones: Kylin 7 (1938); Norris: 41 (1987e).

Thalli usually under 30 mm high and less than 1 mm broad. The upright plants often grow in clusters, have a stoloniferous prostrate system, but usually do not form an extensive turf (Figures 3A; 4E). Thallus texture soft and flexuous with a characteristic relatively bright purplish red colour that makes the plants outstanding in their natural habitat. Thalli often have a few long branches, almost equal

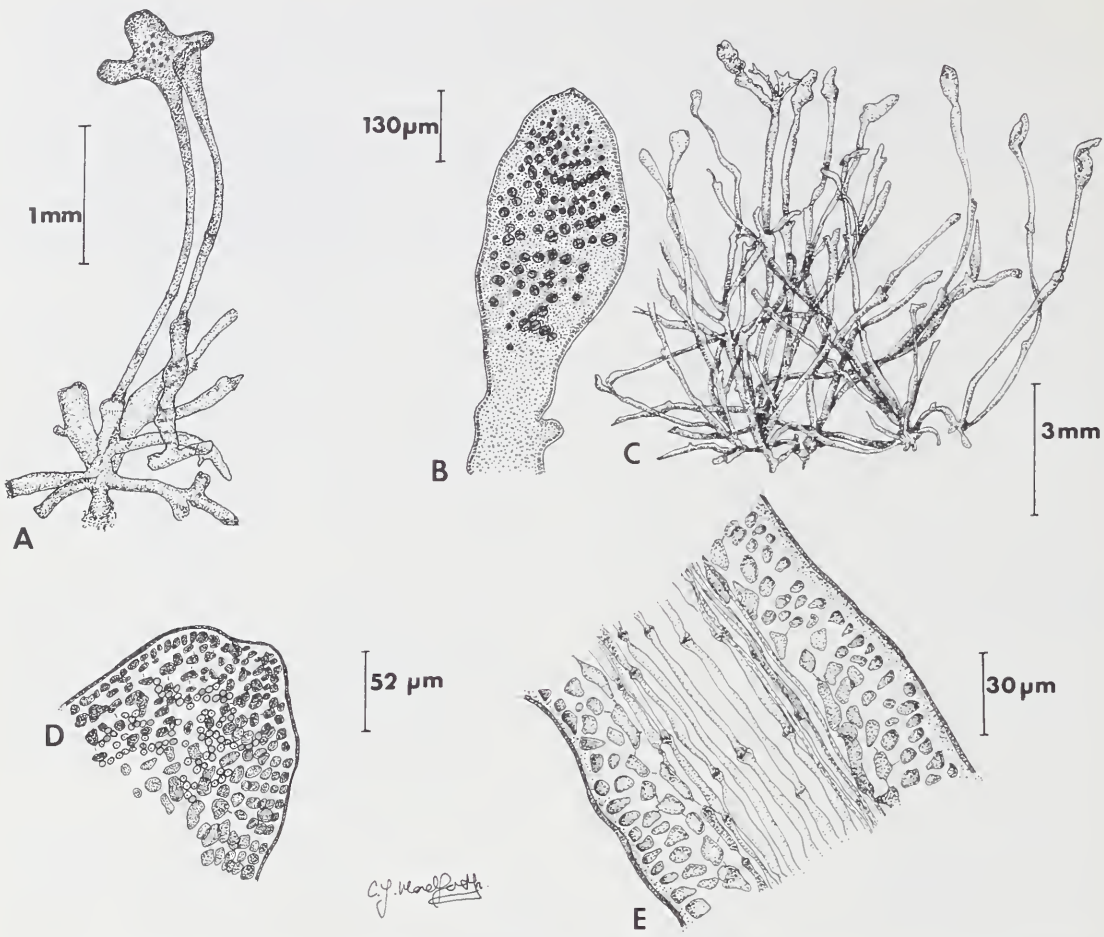

FIGURE 2.—*Gelidium arenarium*. A, part of plant showing attachment and erect tetrasporangial branch; B, flattened fertile branch tip showing tetrasporangial sorus; C, habit of plant, some branch tips bearing tetrasporangia; D, edge of flattened branch showing accumulation of rhizines at margin; E, longitudinal section of branch, two rhizines are present between cortex and medulla.

in length, attached near to one another giving an overall umbellate appearance to the plant (Figures 3D; 4E). Apices of branches usually do not taper to an acute point, but with obtuse ends approximately same diameter as more proximal parts of branch (Figure 4D). Blades may have a series of small proliferous bladelets, distichously arranged, in distal regions, but many branches remain unbranched. Branches often have what appear to be regrowth after grazing or possibly seasonal changes in growth rates (Figures 3A, F; 4E). Blades measure up to 200 µm in cross-sectional view, cortex comprised of three layers, a single layered outer cortex of small cells (up to 15 µm in diameter) and two layers of cells in inner cortex with larger cells (up to 14 µm in diameter) (Figures 3E; 4F). Medulla comprised of colourless cells up to 18 µm in diameter. In the flattened blade medulla is 5–8 layers of cells in thicker regions and may contain rhizines as well as a few filaments of narrow pigmented cells and larger medullary cells (Figure 4F). Rhizines sometimes present only in edges of blades and no rhizines were found in some sections of prostrate branches as well as in upper regions of blades.

Reproduction: distal marginal bladelets often fertile, bearing a single sorus of tetrasporangia (Figures 3B, C; 4A), spermatangia or a single cystocarp (Figure 4C). Tetrasporangia in some branchlets aligned along primary branch axes within blade, with a chevron arrangement (Figure 4A). No more than one ostiole, slightly protuberant, has been observed on cystocarps (Figure 4B, C).

The characteristic of one ostiole, in addition to carposporangia occurring in short chains rather than singly (Fan 1961), were considered to be of basic importance in separating *Pterocladia* from *Gelidium*. Norris (1992a), however, maintained that these and other characters used for separation of these genera are either too flexible or not worthy of separating taxa at generic rank in the Gelidiales. Therefore, species formerly assigned to *Pterocladia* by various authors (Norris 1987e) are returned to *Gelidium*.

Distribution: Natal and possibly in Brazil.

NATAL.—2930 (Pietermaritzburg): Durban, Reunion Rocks, *Nat 1882, 2022*, 16-IV-1984, *NU 9219, 9054*. 2931 (Stanger): Umdloti, on reef, tetrasporangiate, *Nat 1017*, 14-II-1983. 3030 (Port Shepstone): Park Rynie, Rocky Bay, *Nat 441*, 18-X-1982; female, *Nat 1424*, 9-IX-1983.

At the present time this species is known to occur intertidally on the central Natal coast from Mvoti River in

the north to Palm Beach in the south. The plants described by Joly (1965) from Brazil as *Pterocladia americana* seem to be the same as ours. Santelices (1976) transferred the Caribbean plants of *P. americana* to *Gelidium*.

4. **Gelidium caloglossoides** *Howe* in Memoirs of the Torrey Botanical Club 15: 96 (1914). Type: Peru, on shells dredged from 2.5 fathoms near Isla San Lorenzo, *Coker 59 p.p.* (NY).

Pterocladia caloglossoides (Howe) Dawson: 76 (1953).

Pterocladia parva Dawson: 77 (1973).

Icones: Howe: t. 34, 35 (1914); Dawson: t. 6, figs 1, 2 (1953); Abbott & Hollenberg: 350 (1976); Norris: 40 (1987e).

Thalli with cylindrical to compressed prostrate branches attached by peg-like holdfasts to substratum, often at regular intervals of growth, ± 500 μm apart (Figure 5A, B). Upright branches formed at many points of attachment, usually in pairs but sometimes 3–5 present. Some of the upright branches may become repent and continue the prostrate system, but most upright branches determinate, at least temporarily, up to 3 mm long and 100–400 μm broad. Branch tips attenuate abruptly and cortication, at distal regions, occurs in rows above interior axial cell rows of primary laterals (Figure 5E). Thalli have a simple anatomical structure (Figure 5D): outer cortical cells spheroidal to ovoid, up to 12 μm in diameter; inner cortical cells slightly larger (up to 15 × 18 μm); single row of

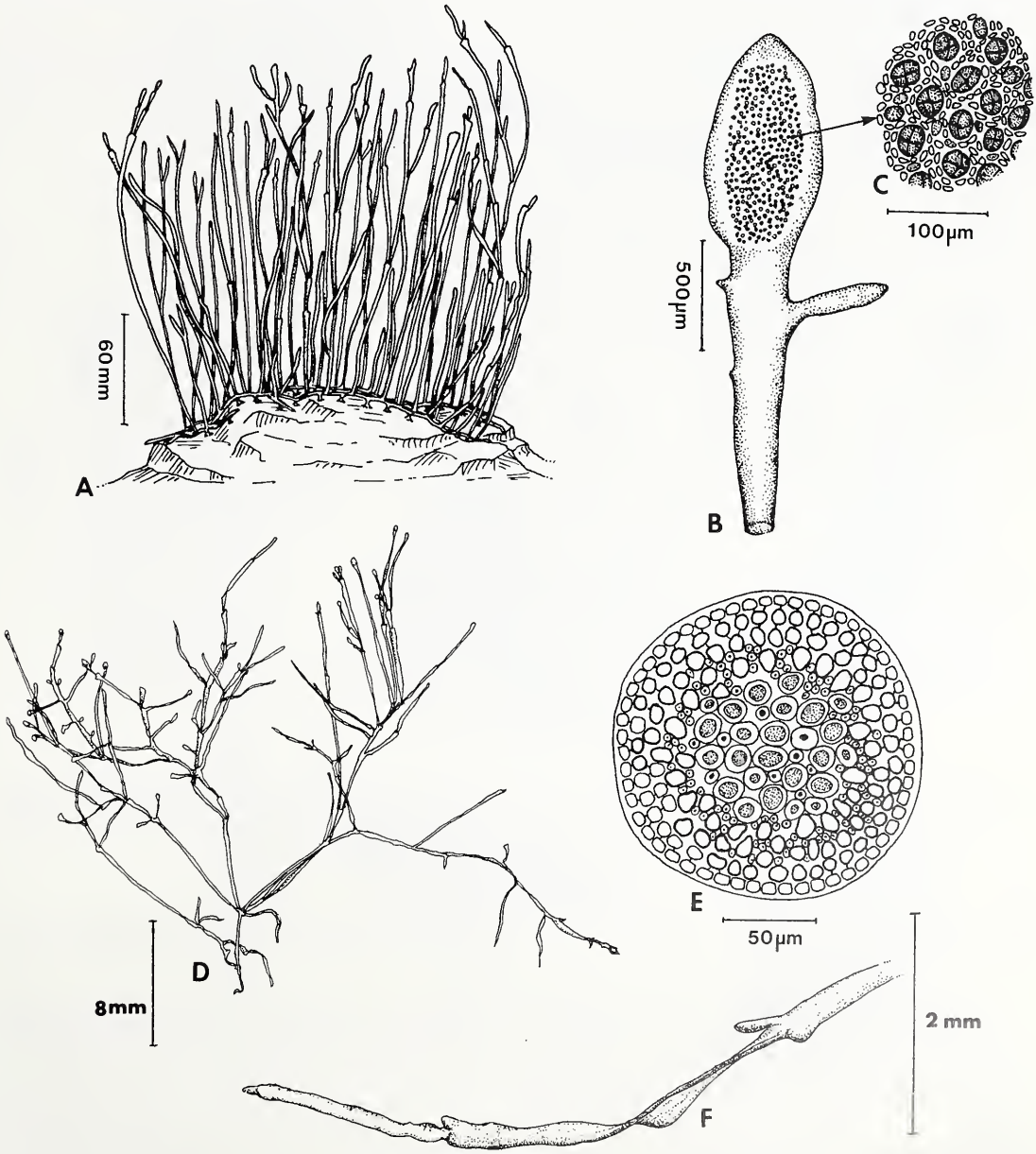

FIGURE 3.—*Gelidium caespitosum*. A, habit of a strongly rhizomatous sterile plant; B, branch tip with tetrasporangial sorus; C, enlargement of part of tetrasporangial sorus, surface view; D, habit of a large highly branched plant; E, cross section of thallus; F, enlarged branch from plant shown in D, showing flattened branch tip.

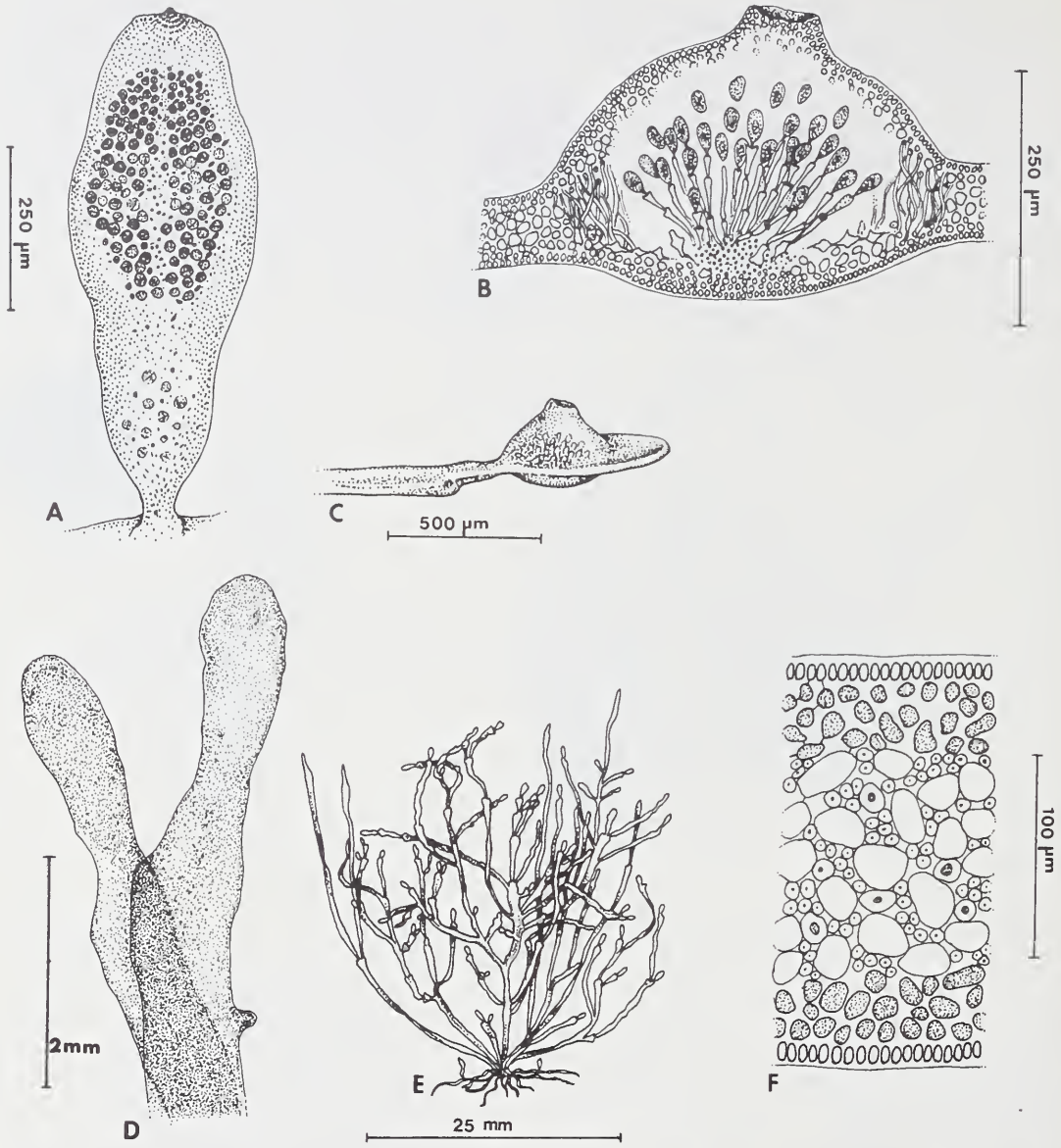

FIGURE 4.—*Gelidium caespitosum*. A, enlarged lateral fertile branchlet showing tetrasporangial sorus; B, cross section of a cystocarp; C, enlarged entire cystocarp on branch tip; D, sterile branch tips showing flattened character; E, entire plant with many flattened branches; F, cross section of thallus.

medullary cells up to 38 × 15 µm. Rhizines occur in small groups in medulla.

Reproduction: broader upright branchlets usually fertile, male branchlets forming spermatangia that completely cover surface except attenuated proximal and distal parts (Figure 5F). Released mature spermatia form a watery gelatinous 'cloud' that envelopes the fertile branch (Figure 5F, G). Tetrasporangia formed in sori that terminate branches, sporangia arranged in regular V-shaped rows (Figure 5C). Carpogonial branches also formed on broader tips of upright branches. Fertile branches can become indeterminate and develop into axes similar to the ones that produced them.

Distribution: Peru north to British Columbia on North America's Pacific coast, Hawaii, Indonesia, Queensland, Natal.

NATAL.—2930 (Pietermaritzburg): Durban, Reunion Rocks, tetrasporangiate, *Nat 2047*, 16-IV-1984, *NU 9418*. 3030 (Port Shepstone): Park Rynie, Rocky Bay, tetrasporophyte, *Nat 2426*, 28-VIII-1984. Cultures of male, female and tetrasporangiate phases were isolated from *Nat 2426*.

Previously unknown in Africa, this species has been recognized as an important turf-forming species on the central Natal coast. Its identity was confirmed only after it was isolated into unialgal culture and all reproductive stages except cystocarp formation were observed in the laboratory.

According to Santelices (1977), *G. caloglossoides* (as *Pterocladia caloglossoides*) is particularly characterized by its 'radially produced, divaricate branches, the occurrence of only one row of medullary cells, the large size of the cortical cells, and the V-shaped arrangement of young sporangia.' The Natal specimens have all of these basic characteristics.

5. **Gelidium capense** *(S.G. Gmelin) Silva ex Silva et al.* in Smithsonian Contributions to the Marine Sciences, No. 27: 26 (1987). Type: South Africa, Cape Province, Cape of Good Hope (LE, holo.—SAM, photo.!).

Fucus capensis S.G. Gmelin: 157 (1768).

Gelidium versicolor (S.G. Gmelin) Lamouroux p.p.: 41 (1813) sensu Seagrief: 31 (1984).

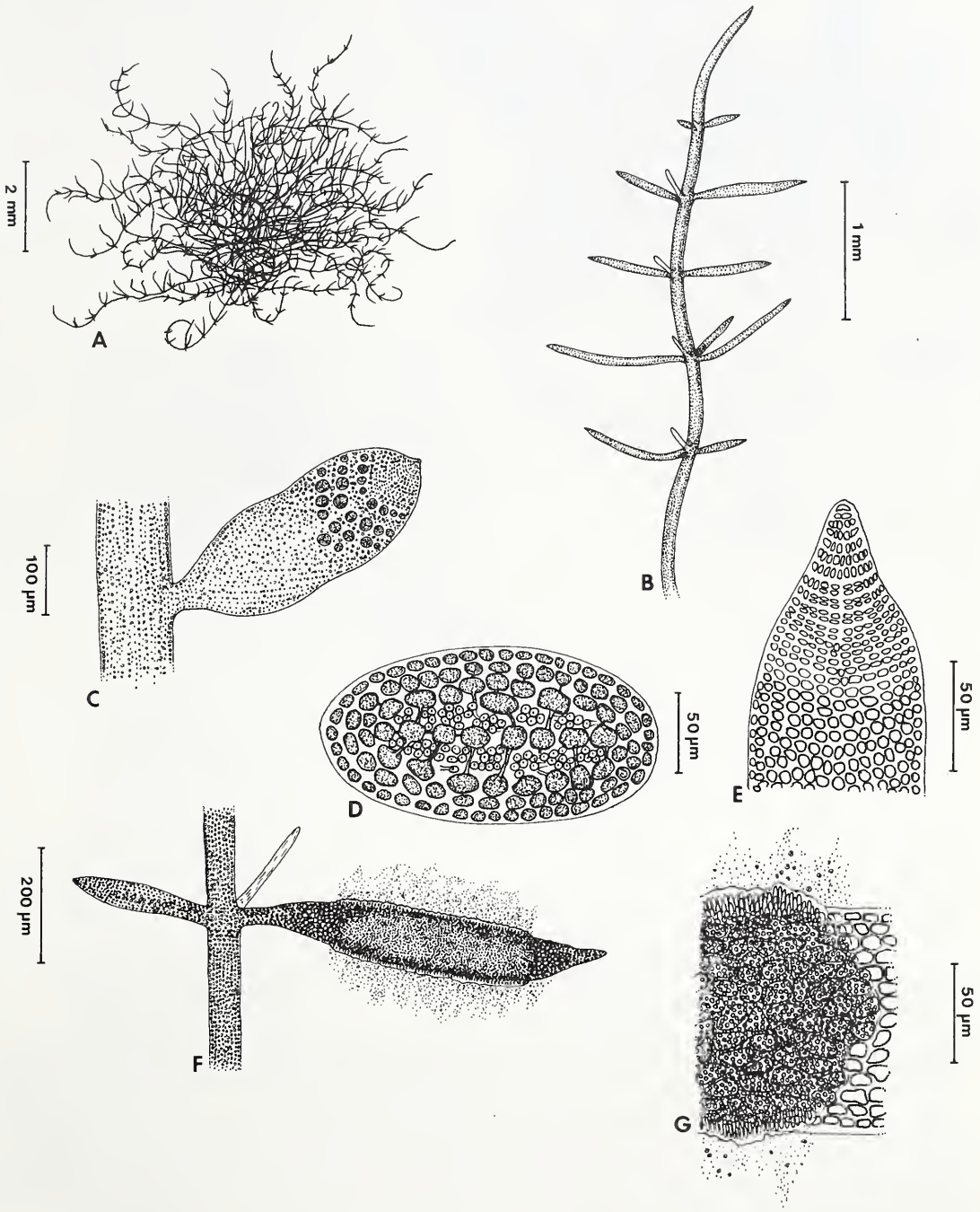

FIGURE 5.—*Gelidium caloglossoides*, all figures made from plants grown in culture. A, habit of plant; B, enlarged branch of plant shown in A; C, tetrasporangiate branchlet, flattened and with tetrasporangia forming chevron-like arrangement; D, cross section of thallus; E, branch tip showing distichous arrangement of cells in thallus near tip; F, male branchlet with released spermatia surrounding branchlet; G, enlargement of margin of branchlet shown in F.

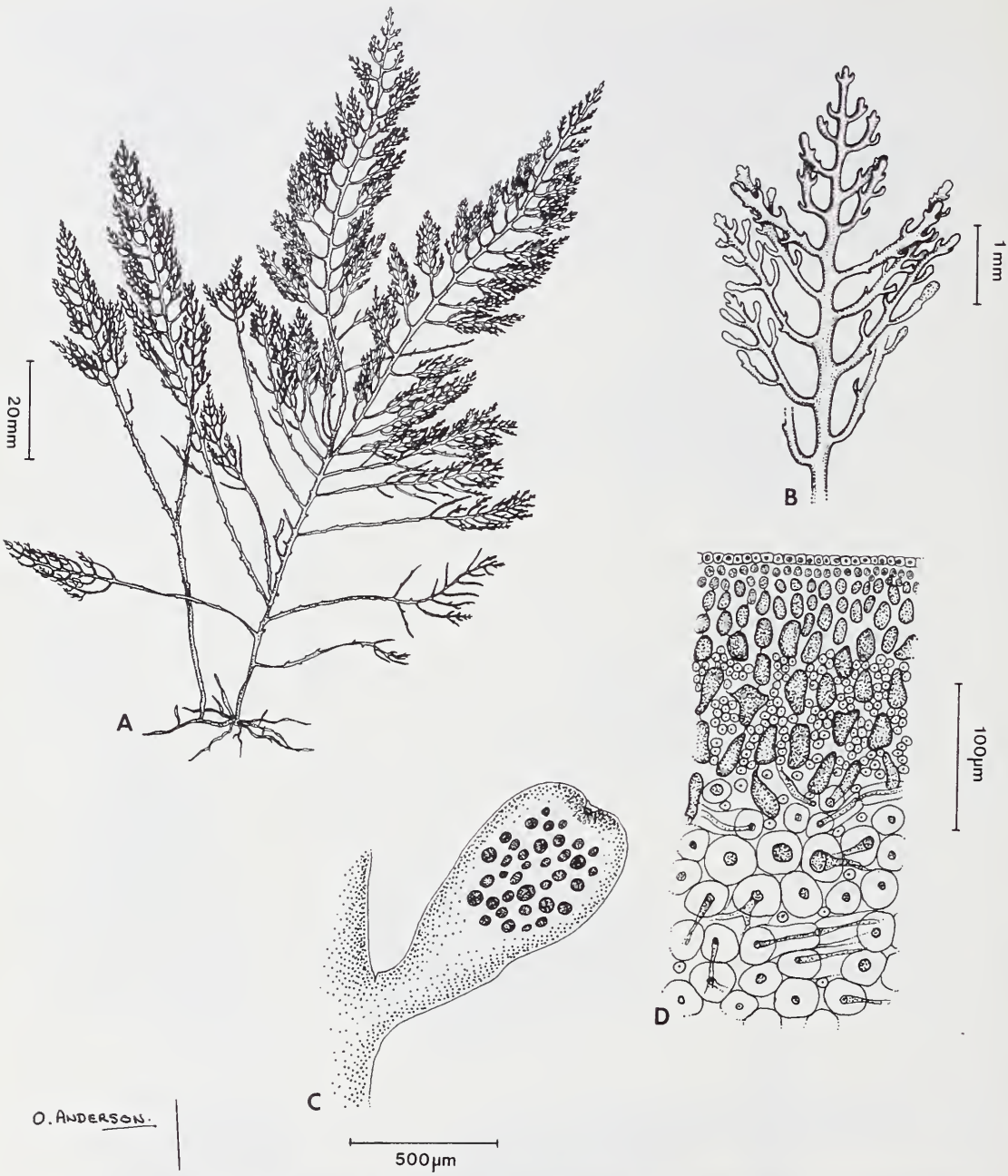

FIGURE 6.—*Gelidium capense*. A, habit of plant; B, enlargement of part of branch, note geniculate bending of branchlets; C, tetrasporangial branchlet; D, part of cross section of thallus.

Icones: S.G. Gmelin: 157, t. XVII, fig. 1 (1768); Norris *et al.*: 379 (1987).

Thalli dark purple to brownish purple, with a prostrate rhizomatous holdfast from which several erect branches emerge (Figure 6A). Erect axes compressed, up to 200 mm high, pinnately branched, branchlets opposite or alternate. Lower regions of axis cylindrical, lower compressed area usually bearing persistent proximal parts of branches that have abcissed, often giving serrations to proximal margin (Figure 6A). Branches often conspicuously geniculate, especially in distal regions (Figure 6A, B). Ultimate vegetative branchlets mostly less than 0.5 mm broad, usually with serrate margins and often congested. Outer cortical cells up to 8 μm in diameter. Inner cortical cells up to 10 μm in diameter, separated by large bundles of rhizines each of which may be up to 3 μm in diameter. Medulla with large rounded cells up to 25 μm in diameter (including wall), isolated or small groups of rhizines usually present between large cells (Figure 6D).

Reproduction: tetrasporangia occur on small branchlets up to 1.5 × 0.7 mm (Figure 6C). Cystocarpic plants have not been found in Natal.

Distribution: South Africa.

NATAL.—3130 (Port Edward): Palm Beach, tetrasporangiate, *Lamont 2*, V-1979, *NU 8502*.

Rare in Natal, occurring only in the southern border region. Saxicolous, low intertidal to subtidal. This species seems to be the most common one in the Cape of Good Hope and Cape Agulhas region. There is some difficulty in separating some specimens of *G. capense* from fertile specimens of *G. abbottiorum*, particularly specimens from the eastern and southern Cape regions. Further research may show that environmental factors have influence on structure of these plants or that hybridization may be occurring between species. The form of *G. capense* is the same as *G. robustum* (Gardner) Hollenberg & Abbott from California and it is recommended that a study be made on the possibility that these two species, although occurring remote from one another, may be the same.

6. **Gelidium minusculum** *(Weber-van Bosse) R.E. Norris*, stat. nov.

Gelidium pusillum var. *minuscula* Weber-van Bosse: 226 (1921); Feldmann & Hamel: 239, fig. 20 (1936). Type: Indonesia (L?).

Icones: Feldmann & Hamel: fig. 20 (1936). Other published illustrations that appear to be this species are: Joly, pl. 19, figs 274–276 [as *G. pusillum* var. *minusculum*] (1965); Cribb, pl. 7, fig. 5 [as *Pterocladia caloglossoides*] (1983).

Thallus a creeping cylindrical branching system, branches up to 100 μm in diameter, from which emerge simple, flattened lanceolate upright branches (Figure 7A, B), formed at more or less regular intervals along axis, often associated with rhizoidal branches that attach thallus. Rhizoidal branches and upright branches may not always emerge from opposite positions, each sometimes occurring individually. Broadest part of upright branch usually not more than 500 μm broad, branches up to 2 mm long. Blade with rhizines in medulla (Figure 7C) but missing

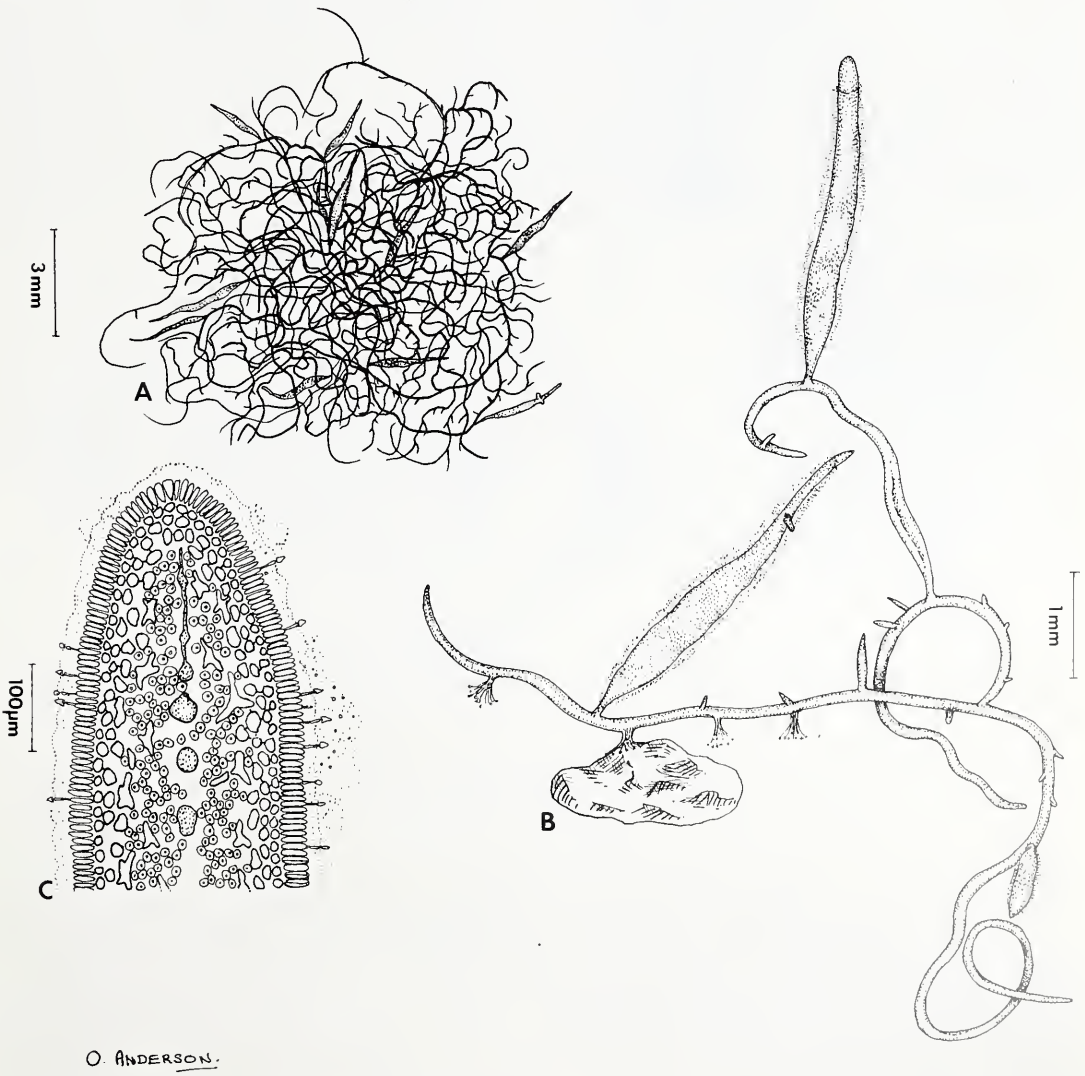

FIGURE 7.—*Gelidium minusculum*, all figures made from plants grown in culture. A, habit of plant; B, enlargement of plant showing flattened male upright branchlets; C, cross section of male fertile region.

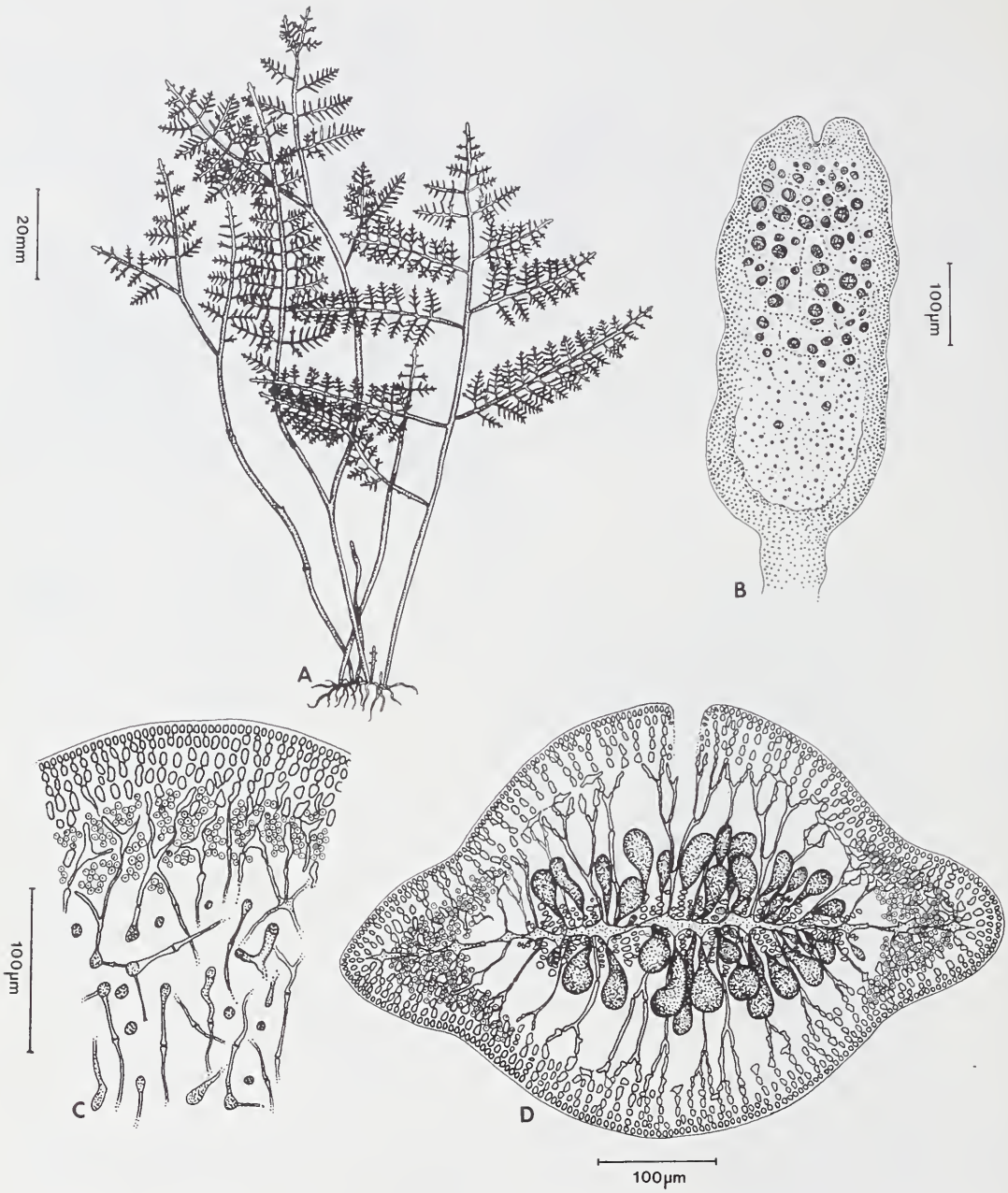

FIGURE 8.—*Gelidium pteridifolium*. A, habit of plant; B, tetrasporangial branchlet; C, part of cross section of thallus; D, cross section of cystocarp. (Courtesy of the *South African Journal of Botany*.)

in thinner parts of blades and in young regions of thallus. Outer cortical cells up to 10 μm in diameter.

Reproduction: only a male plant of this species has been collected in Natal, with entire upright branch covered with spermatangia (Figure 7B). Spermatia, cut off transversely from palisade-like bearing cells, penetrate the gelatinous matrix, leaving a conspicuous channel, and released into watery gelatinous material surrounding branch, forming a cloud-like envelopment (Figure 7C).

Distribution: Mediterranean, Indonesia, Brazil, Queensland, Natal.

This small species of *Gelidium* is probably common in Natal but it is rarely recognized because of its small size and its form similar to other small species of the Gelidiales. It is recorded with certainty only from the Mvoti River region, north of Durban, *Nat 2440*, 16-III-1984, from where a culture of a male plant has been established.

Possible confusion of non-reproductive plants of *G. minusculum* with similar plants of *Gelidium caloglossoides* may occur because of the similar habits of both species. The rarity of paired upright branchlets in *G. minusculum* compared with their usual occurrence in *G. caloglossoides* is a useable distinguishing criterion in addition to the more

irregular placement of rhizoidal bundles in the former species.

7. **Gelidium pteridifolium** *R.E. Norris, Hommersand & Fredericq* in South African Journal of Botany: 375 (1987); Hommersand & Fredericq: 254 (1988). Type: Natal, Palm Beach, near Port Edward, *Pienaar 634* (NU, holo.).

Thalli reddish purple, up to 200 mm high, with prostrate determinate rhizomatous holdfast from which many upright branches emerge (Figure 8A). Upright branches with flattened axis except in most proximal region where it abruptly tapers to a narrower cylindrical conjunction with holdfast; with many distichously arranged pinnate branches, particularly in distal regions, proximal axis usually without branches and with entire margin. Branches with evenly spaced (1–2 mm) short determinate branchlets, often oppositely arranged and all ± same size, with entire margins; emerging at almost right angles from axis, not geniculate; terminating in bluntly to acutely pointed, often tripartite tips. Outer cortical cells (Figure 8C) up to 6 μm in diameter, inner cortical cells up to 10 μm in diameter. Most internal cortical cells become angular and attach to long arms of medullary cells. Large bundles of rhizines present between inner cortical cells, no rhizines present in medulla which is comprised mostly of angular cells, up to 25 μm in diameter (including wall), that are united into filaments (Figure 8C).

Reproduction: tetrasporangial branchlets inverted cordate to elliptical (Figure 8B), usually with a deep and conspicuous apical incision, up to 1.0 × 0.5 mm. Cystocarps biloculate (Figure 8D), subterminal in ultimate cylindrical branchlets, occupy a much broadened section 0.5 mm in diameter. Long distal beak-like extension of branchlet usually present distal to cystocarp.

Distribution: South Africa from the Cape of Good Hope to southern Natal.

NATAL.—2930 (Pietermaritzburg): Durban, Reunion Rocks, *Nat 1831*, 16–IV-1984; Isipingo, female, *Ward 814*, III-1949, *NU 8513*. 3130 (Port Edward): Palm Beach, tetrasporangiate and female, *Nat 1143*, 15-V-1983, *NU 7112, 8763*.

The distinctive robust nature of this species and the flattened pinnately branched laterals arranged closely together on branches allow it to be relatively easily separated from *G. abbottiorum*. Non-geniculate branchlets spreading at right angles from the axes are quite different from the branching pattern of *G. capense*, a species having many more overlapping branchlets in distal regions, and also with geniculate bending of most branchlets.

8. **Gelidium reptans** *(Suhr) Kylin* in Lunds Universitets Årsskrift, Ny Följd, Andra Afdelningen 34,8: 6. (1938). Type: South Africa, Cape of Good Hope (B, dest.?; isotypes LD!, S, –SAM photo.!).

Phyllophora reptans Suhr: 285 (1841).

Icones: Suhr: pl. 3, 10 (1841); Kylin: 7 (1938).

Thalli dark purplish red, with indeterminate prostrate system of cylindrical branches which produces thin, flat upright determinate branches up to 25 × 1 mm (Figure 9A, F). Upright branches are undivided blades in young stages but often irregularly pinnately branched in later stages, branching often occurring after injuries. Cortex 2–3 layers of small cells; medulla comprised of thick-walled larger cells in filaments and numerous rhizines (Figure 9E).

Reproduction: tetrasporangia produced in ill-defined sori in primary upright blades; older branched thalli forming distinct sori on lateral branchlets (Figure 9D). Cystocarps in distal regions of main upright branch or in branchlets (Figure 9B), with two ostioles, biloculate, up to 300 μm in diameter (Figure 9C).

Distribution: locally common in Natal, often forming a distinctive turf on rocks or intertidal shellfish.

The relatively thin, membranous blades terminated by a single apical cell and distichous branching in older thalli characterize this species.

MOZAMBIQUE.—2632 (Bela Vista): Inhaca Island, Barreira Vermelha, *Papenfuss & Scagel, 110E-PR-XXVI-15*, 12-XI-1962, (UC, UBC).

NATAL.—2832 (Mtubatuba): Cape Vidal, *Nat 5241*, 25-V-1987, *SAM 100430*; Mvoti, *Nat 1626*, 17-III-1984, *SAM 100424, 100425*. 2930 (Pietermaritzburg): Durban, Reunion Rocks, *Nat 1795, SAM 100429*; Isipingo, *T.A. Stephenson s.n.*, July 1935, *SAM 100428*. 2931 (Stanger): Chaka's Rock, *Papenfuss & Scagel, 110E-PR-XXXIII-62*, 26-XI-1962, (UC, UBC). 3030 (Port Shepstone): Park Rynie, Rocky Bay, *Nat 1423*, 9-IX-1983, *SAM 100427*; Umpanagazi, 2-V-1939, *Ecol. Surv. G.4.F., SAM 100432*.

CAPE.—3227 (Stutterheim): East London, beach, *Ecol. Surv. L.4.8, SAM 110433*.

Gelidium reptans is a common small species of this genus in Natal, occurring on shells in many intertidal regions that have been sampled. In addition to Suhr's (1841) original figure of this species, there are other published illustrations that are similar: Kützing (1868): pl. 37i–h [as *Acrocarpus pulvinatus* Kützing]; Feldmann & Hamel (1936): fig. 19c [as *Gelidium pusillum* var. *pulvinatum* (Agardh) Feldmann]; Egerod (1971): figs 32–37 [as *Gelidium pusillum* (Stackhouse) LeJolis]; Santelices (1977): fig. 4c–e [as *Gelidium pusillum* proximum var. *cylindricum* Taylor].

Børgesen (1943) considered *Gelidium reptans* to be the same taxon as *Gelidium pusillum* var. *pulvinatum*. I do not agree with this synonymy because of anatomical differences and because the tetrasporangial sori of the latter taxon are not usually borne separately in bladelets and are not so clearly defined as in *G. reptans*.

ONIKUSA

Onikusa *Akatsuka* Botanica Marina 29: 63 (1986). Type species: *O. pristoides* (Turner) Akatsuka.

Thalli comprised of cylindrical prostrate indeterminate rhizomatous branches and erect, foliose to ligulate determinate blades, often with a midrib; margins lobed, entire to denticulate or serrate, sometimes with marginal branchlets but most indeterminate branches originating on midrib or blade surface forming a ramisympodial system; other small surface proliferations sometimes present but usually

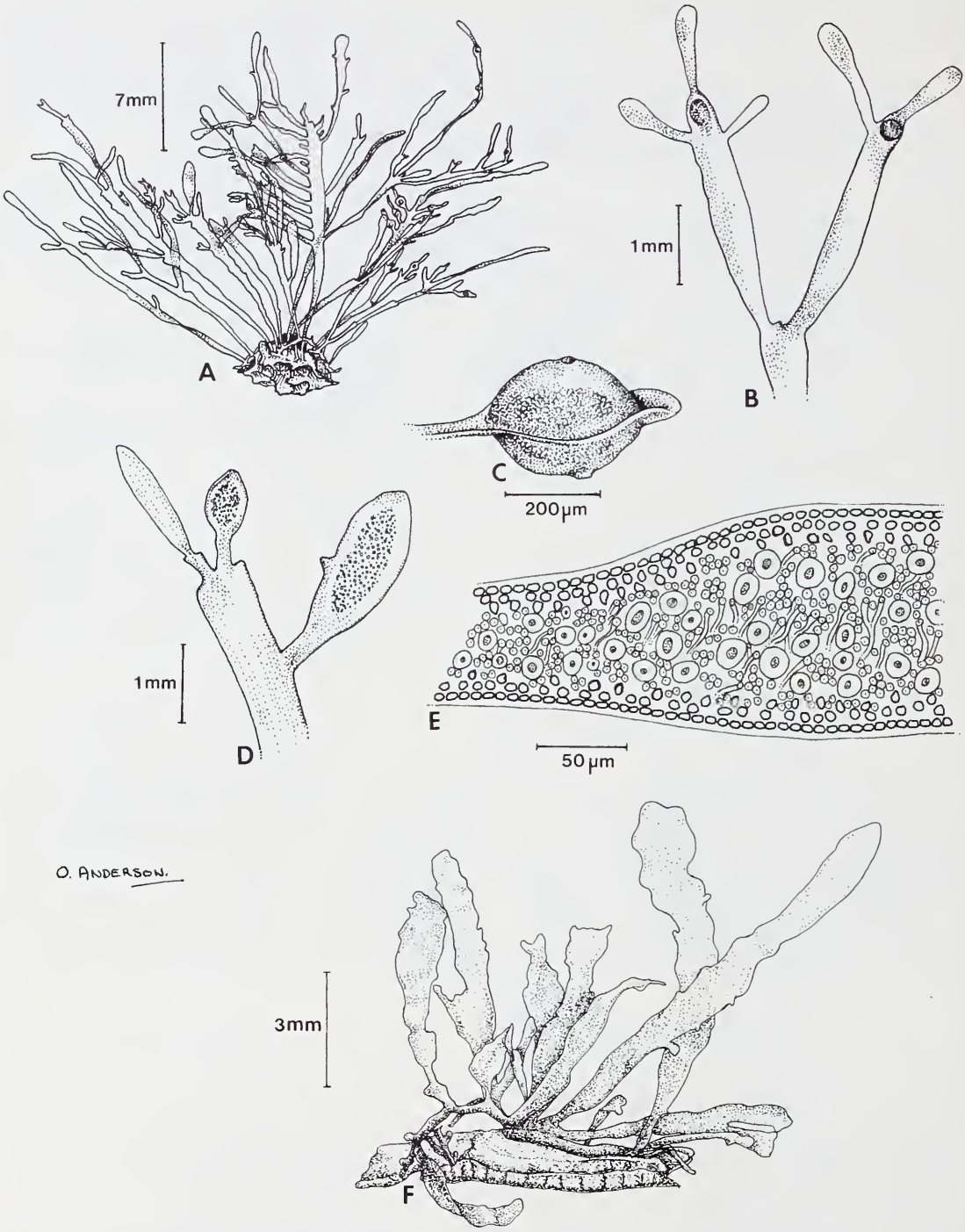

FIGURE 9.—*Gelidium reptans*. A, thallus habit showing pinnate branching of one branch; B, branch tip showing two cystocarps; C, enlargement of cystocarp, note ostioles on opposite sides; D, tetrasporangial branchlets; E, cross section of thallus; F, enlargement of prostrate system and upright branches.

sparse. Several active apical cells present on distal determinate branch margins during period of growth. Outer cortical cells occur in tetrads when viewed from surface in certain, particularly younger, regions of upright thallus. Inner cortical cells usually angular, not greatly enlarged; often with interspersed rhizines which may also occur in medulla.

Reproduction: cystocarps bilocular, occurring on branchlets of upright system in ligulate species, but in distal regions on main blade of foliose species. Spermatangia produced in positions similar to cystocarps. Tetrasporangia, known less commonly than bisporangia, occurring in diffuse sori in distal parts of blades or on proliferous bladelets in ligulate species.

Key to Natal species of *Onikusa*

1a Thalli small, up to 10 mm high, producing a low turf on surfaces of intertidal shells, including barnacles. Blades entire when young but becoming irregularly lobed or sometimes pinnately lobed in older stages of development. Indeterminate branches usually lacking, but formed on blade surface if present. Distal blade margin usually with several transversely dividing apical cells ..... *O. foliacea*

1b Thalli up to 130 mm high, ligulate with a midrib, growing in extensive intertidal colonies on rocks and shells. Alae usually dentate or serrate, often with marginal bladelets that become fertile; indeterminate branches formed adventitiously on midrib. Meristematic area distal, with 1–2, transversely dividing apical cells ..... *O. pristoides*

1. **Onikusa foliacea** *(Okamura) R.E. Norris*: 151–172 (1992a). Type: Japan, on barnacles at Shisô-dima, Seto, Prov. Kii, *Okamura s.n.* (iso., LD!).

Gelidium pusillum forma *foliaceum* Okamura: 51 (1934); Norris (1992a).

Thalli perennial, producing a turf on shells, with prostrate system of cylindrical to compressed indeterminate branches, forming at irregular intervals, broad erect determinate blades ± 10 mm high (Figures 10A; 11A). Several active apical cells (Figure 10D) formed in early stages of development of erect blade, growth activity of this region produces a single lobed and contorted blade that is not pinnately branched. Continued growth of erect blade and erosion of lower regions may eventually produce an irregularly to pinnately branched erect system with a caulescent lower region, distal areas irregularly palmately branched forming undulate blades with entire to erose or crispate margins. Ramisympodial branching of upright system may occur by development and growth of meristem toward distal central part of blade or on thickened axis, the result of erosion of blade margin (Figure 11A). Thalli ± 200 μm thick in section, rhizines 2 μm in diameter, in entire medullary region (Figure 10F, H, I). Other medullary cells stellate, with long slender arms that connect with similar cells throughout tissue. Middle regions of stellate cells up to 5 μm in diameter. Outer cortical cells narrow cuneiform, broader outer side up to 3 μm, cells ± 8 μm long; in some regions of thallus, especially in young areas, may occur in tetrads when viewed from surface. Inner cortical cells spheroidal to angular, 6–7 μm in diameter. Cellular hairs (Figure 10C, I) were found in cortices of many thalli.

Reproduction: tetrasporangia not found but monosporangia or bisporangia (Figure 10H) developed in sori that are ill-defined in broad blades, but often develop in distal parts of blade lobes or in proliferous bladelets (Figure 10G), Male sori formed in similar positions (Figure 10E). Female plants with biloculate cystocarps (Figure 10B), 400–500 μm in diameter, usually formed near marginal lobed areas of upright blades.

Distribution: Japan, apparently only known at Seto; east and southern coasts of South Africa from Natal to Cape Town.

NATAL.—2832 (Mtubatuba): Mvoti River mouth, on shells on reef, male, female and tetrasporangiate, *Nat 1626*, 16-III-1984, *NU 8338, 8344*. 2931 (Stanger): Umpangazi, on shells on reef, *Ecol. 2G.4.F., NU 7876*; Umdloti, on shells on reef, tetrasporangiate, *NU 3123*, 9-II-1981. 3130 (Port Edward): Palm Beach, near Port Edward, on shells on reef, tetrasporangiate and female, *Nat 3983*, 24-V-1986.

Onikusa foliacea is locally common in Natal, often forming a distinctive turf on barnacle shells. The plants figured by Okamura (1934: pl. 17, figs 3 & 4) and Børgesen (1943: fig. 1) are similar to those in Natal in having a broad upright blade.

It is possible that we have a new species in Natal rather than the same one described from Japan by Okamura. The Japanese plants described by Okamura were sterile but the foliose upright system and the habit and habitat strongly suggest that they may be the same as the Natal taxon. More extensive studies are needed, especially on Japanese plants.

2. **Onikusa pristoides** *(Turner) Akatsuka* in Botanica Marina 29: 63 (1986).

Fucus pristoides Turner: 83 (1808).
Sphaerococcus pristoides C. Agardh: 234 (1822).
Delesseria pristoides Lamouroux: 38 (1813).
Phyllophora pristoides Greville: 56 (1830).
Suhria pristoides J. Agardh: 479 (1851).
Gelidium pristoides (Turner) Kützing: 407 (1843); Seagrief: 30 (1984).
Icones: Turner: pl. 39 (1808).

Thalli ligulate, up to 130 mm high, mostly ± 1 mm broad but some branches up to 2 mm wide (Figure 11B). Distinct midrib present on most main branches, often extending almost to branch apex. Distal region with numerous distichously arranged determinate branchlets, most becoming fertile, each with undulate margins, dentate to serrate (Figure 12A, B). Some pinnae becoming indeterminate in growth but most indeterminate branches originate on midrib surface (Figure 11B) forming a ramisympodial system. Older thalli very bushy with adventitious branches as well as fertile branchlets.

Reproduction: cystocarps protruding from both surfaces of alae (Figure 12A, C), usually with two ostioles. Bisporangia located in expanded branchlets (Figure 12B), which may be either primary pinnae or may develop adventitiously. Bisporangia in central sori in branchlet, usually with extensive marginal sterile tissue, including many rhizines (Figure 12D). Male reproduction not observed.

A distinctive thallus with strongly undulate margins on bushy ligulate branches, it often grows in extensive intertidal colonies. The type species of the genus, *Onikusa pristoides* is important as an agarophyte in South Africa, and is common on the east and south coasts of South Africa, but it occurs barely within the Natal southern border, in the vicinity of Port Edward (Ouma's Pool, Port Edward, 1-III-1990, legit *A. Critchley s.n., Nat 7165*).

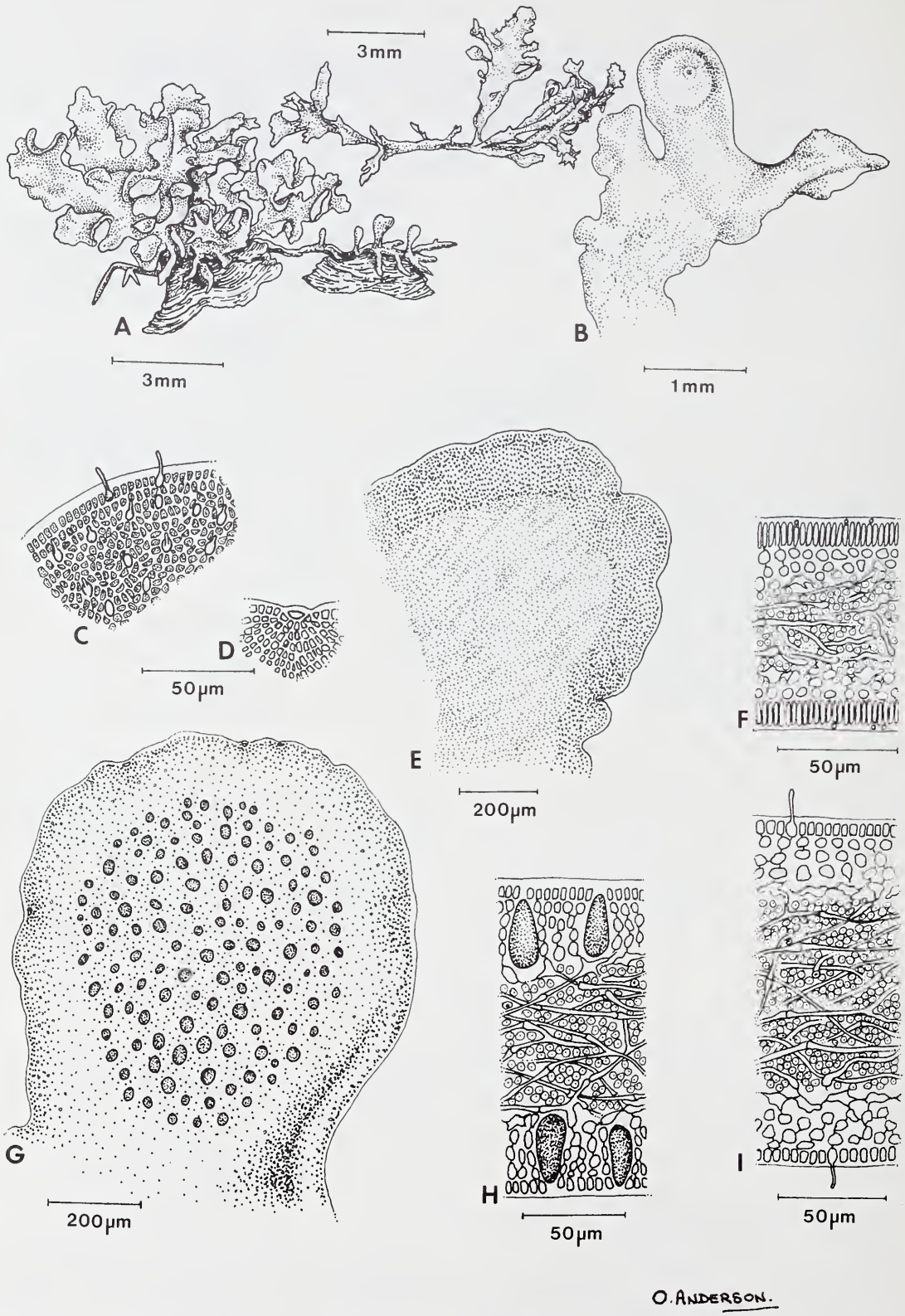

FIGURE 10.—*Onikusa foliacea*. A, habit of young thallus growing on barnacles, note proliferations from thallus surface are uncommon; B, cystocarps on thallus lobes; C, thallus margin showing hairs growing from cortical cells; D, branch tip showing apical cell; E, tip of male branchlet; F, cross section of male sorus; G, marginal proliferation bearing a sporangial sorus; H, cross section showing monosporangia; I, cross section of vegetative part of thallus showing hairs on two cortical cells.

PTILOPHORA

Ptilophora *Kützing* in Botanische Zeitung 5: 25 (1847). Type species: *P. spissa* (Suhr) Kützing.

Beckerella Kylin: 139 (1956).

Thallus perennial, upright with determinate rhizomatous, but sometimes stoloniferous holdfast; not forming extensive continuous colonies. Some species often associated with sponges that may almost completely cover erect branches. Upright branches repeatedly branched, often blade-like and usually with prominent midrib, sometimes a vein extending most of length of thallus. Alae may be absent from proximal parts of older plants. In some species part of thallus covered by papillate or transverse scale-like outgrowths but these may be absent in distal branches or in most or all parts of other plants. Branching marginal or from surface of plant, some species with branches emerging from both regions. Thalli up to 500 mm high, blades up to 10 mm broad. Mature regions of thallus axes with distinct cortical region of small outer cells bordered by an internal layer of rhizines with interspersed filaments of thinner-walled cells growing through tissue to internal cortex of large spheroidal cells. Medulla usually thick with longitudinally directed filaments, sometimes with interspersed rhizines. Young blades with thin filamentous medulla bordered by layers of large spheroidal cells adjacent to small outer cortical cells. Rhizines often absent from thin blade regions.

Reproduction: reproductive structures borne in sori on marginal proliferations or from surface proliferations on blades or midrib; they have the same structural characteristics as in *Gelidium*.

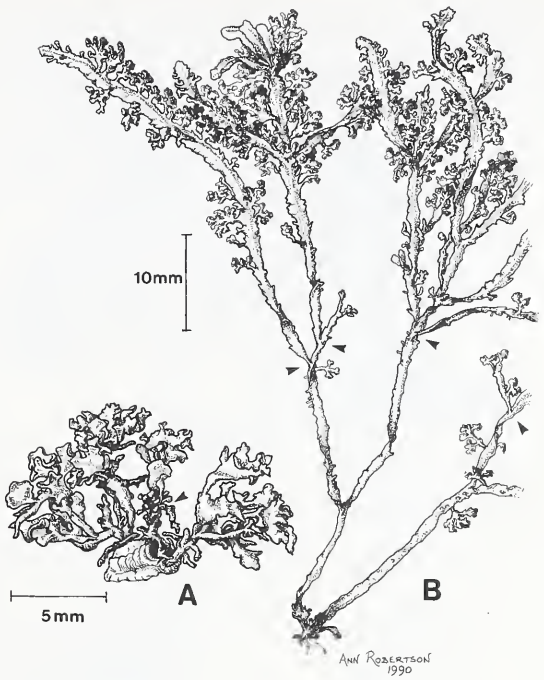

FIGURE 11.—A, *Onikusa foliacea*, habit of older plant on a calcified worm tube, note proliferations from thallus surface (arrow), some of them continuing the growth of thallus; B, *Onikusa pristoides*, habit of older plant with sympodial branching from thallus surface proliferations (arrows). (Courtesy of California Sea Grant Publications on Economic Algae, Vol. 3.)

Key to Natal species of *Ptilophora*

1a Marginal determinate and indeterminate vegetative branches regularly produced. Midrib usually indistinct distally:
2a Axis broad (up to 7 mm), distal branches often quercifoliate:
3a Marginal determinate branches narrow, usually simple, occasionally tri- or quadridentate but more often elongate with obtuse tips and without midrib ..... 6. *P. rumpii*
3b Determinate lateral branches broad and tridentate to pinnately branched, sometimes with a midrib 4. *P. pinnatifida*
2b Axis (midrib + alae) narrow (up to 2 mm broad), pectinate; determinate lateral branches often unbranched, rostrate to acuminate:
4a Plants up to 300 mm tall, midrib present but often interrupted ..... 3. *P. pectinata*
4b Thalli up to 60 mm tall in Natal, midrib absent ..... 2. *P. hildebrandtii*
1b Main branches elongate and often unbranched for long distances except for marginal short fertile branchlets; midrib usually extending to branch tips:
5a Determinate vegetative branches absent or sparse; thalli with elongate unbranched distal branches; surface proliferations, if present, on both midrib and alae; primary branches produced by division of apical cell or, secondarily, by adventitious development from blade or midrib ..... 1. *P. diversifolia*
5b Marginal determinate vegetative branches often produced; primary branches from margins, usually by renewed growth of determinate laterals:
6a Blades broad (up to 10 mm), marginal blades sparsely and irregularly arranged, not forming a regularly pinnately branched thallus. Surface proliferations unknown ..... 5. *P. rhodoptera*
6b Blades 3–5 mm broad, marginal branches numerous and often in a series giving a more or less pinnate aspect to plant. Surface proliferations common and occurring mostly on midrib ..... 7. *P. spissa*

1. **Ptilophora diversifolia** *(Suhr) Papenfuss* in Botaniska Notiser: 214 (1940); Seagrief: 49 (1984); Fan: 323 (1961); Norris 251 (1987h). Type: Natal, between the Umtentu and Umzimkulu Rivers, *Drège s.n.* (B, lecto.–UC, photo.!).

Phyllophora diversifolia Suhr: 262 (1840).

Icones: Papenfuss: 215 (1940); Fan: 357 (1961); Norris 245, 246 (1987h).

Thallus perennial, coriaceous and often at least partly covered by a sponge (Figure 13A). Proximal axes cylindrical because of secondary cortication, but compressed to flat and with midribbed alae in distal regions. Many specimens have scale-like processes transversely orientated on blade and midrib in both distal and more proximal regions (Figure 13E). Other thalli may be almost completely devoid of outgrowths on thalli except marginal proliferations bearing reproductive structures. Thalli up to 300 mm tall and branches up to 5 mm broad; margins of blades are entire to undulate. A distinguishing characteristic for this species is the tendency for it to form elongate distal branches that do not produce indeterminate laterals, thereby remaining mostly unbranched. It is not uncommon to find such branches that are 100 mm long.

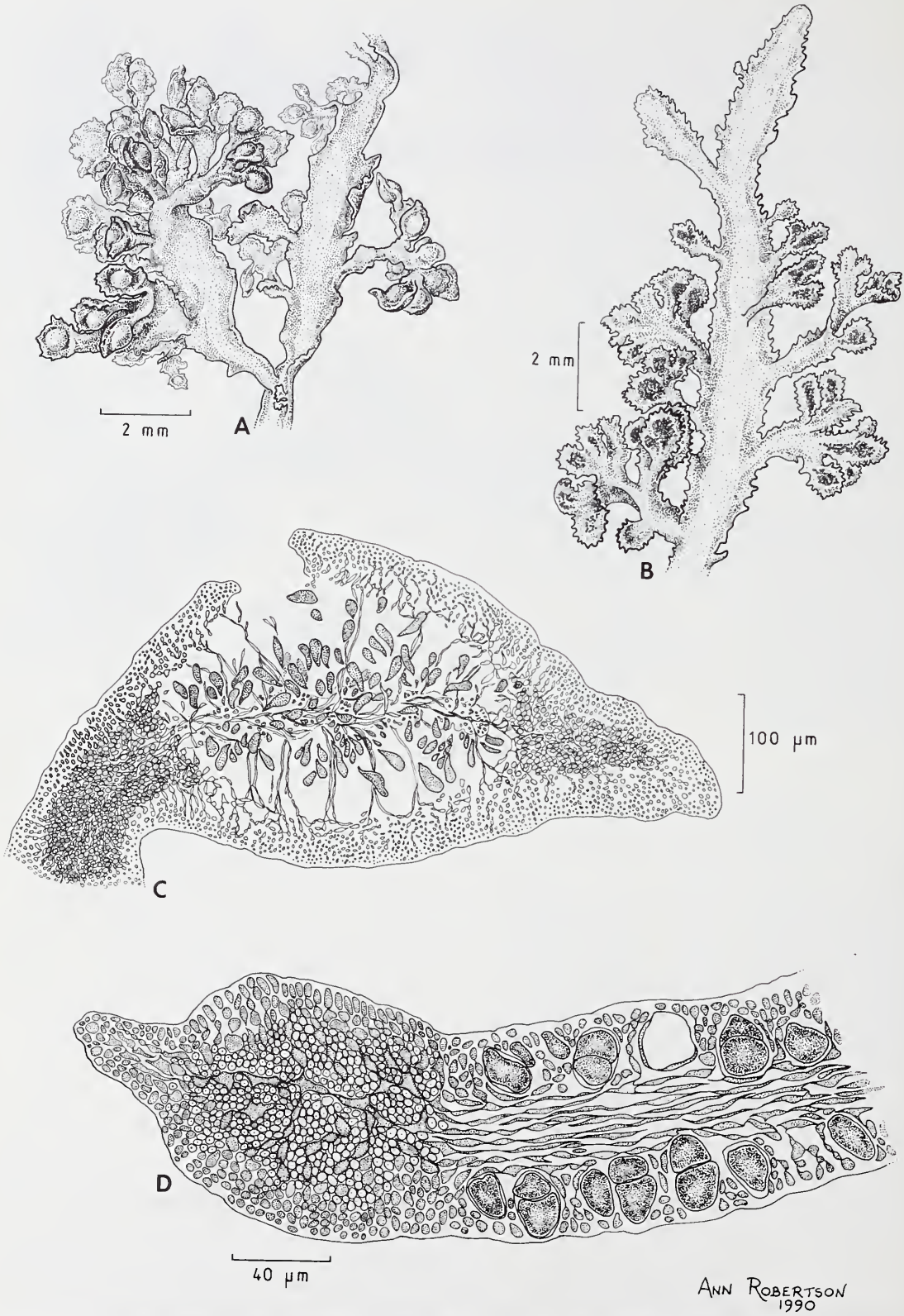

FIGURE 12.—*Onikusa pristoides*. A, part of thallus with bladelets bearing cystocarps; B, part of thallus with tetrasporangial bladelets; C, cross section of cystocarp; D, cross section of tetrasporangial sorus, note absence of rhizines in fertile regions of both C & D.

In distal branches that are not covered by scale-like outgrowths, midrib prominent and margins entire to crenulate (Figure 13A, E). Young blades with ellipsoid outer cortical cells in a single layer (Figure 13D), several inner cortical layers of smaller spheroidal cells and a large-celled medulla. In older regions medullary tissue of large cells displaced by rhizines and narrow-celled medullary filaments that form a central layer in thallus (Figure 13C). Packets of rhizines also produced in inner cortical region, and outlined by secondarily produced narrow-celled filaments.

Reproduction: fertile bladelets, either cystocarpic or bearing tetrasporangial sori, produced marginally on distal parts of thalli or, less commonly, from surface proliferations (Figure 13B, E). Special fertile bladelets always produced and direct conversion of surface proliferations to fertile bladelets does not seem to occur. Usually only one cystocarp (Figure 13B, F) occurs on each bladelet, each being biloculate.

Distribution: southern Natal to northeastern Cape Province.

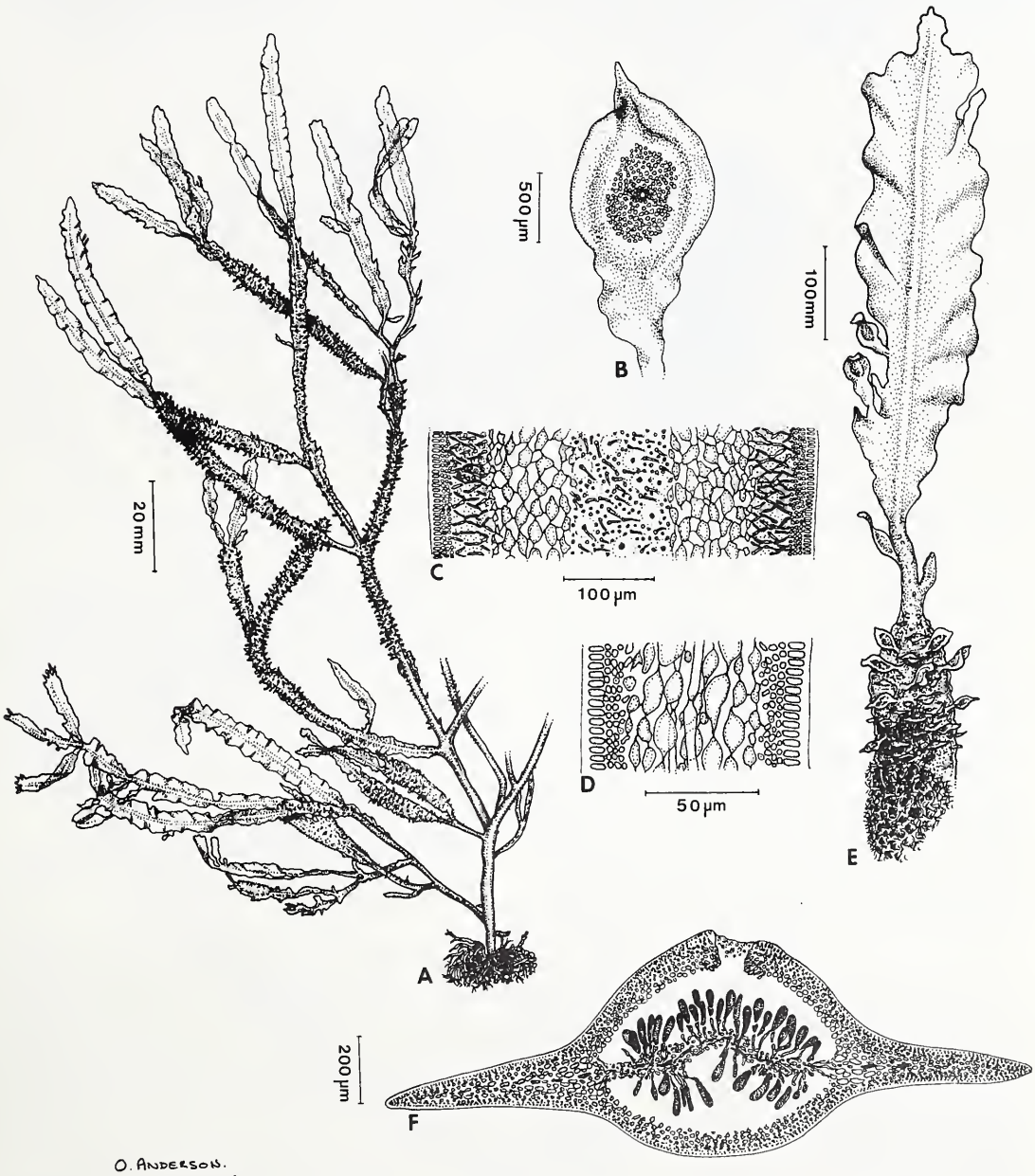

FIGURE 13.—*Ptilophora diversifolia*. A, habit of plant, note numerous proliferations of some proximal parts of branches where sponge infestation is particularly common.; B, branchlet bearing a cystocarp; C, cross section of thallus in mature thick region; D, longitudinal section of ala; E, blade bearing marginal cystocarpic branchlets and surface bladelets in proximal region where sponge is present; F, cross section of a cystocarp. (Courtesy of *Botanica Marina*.)

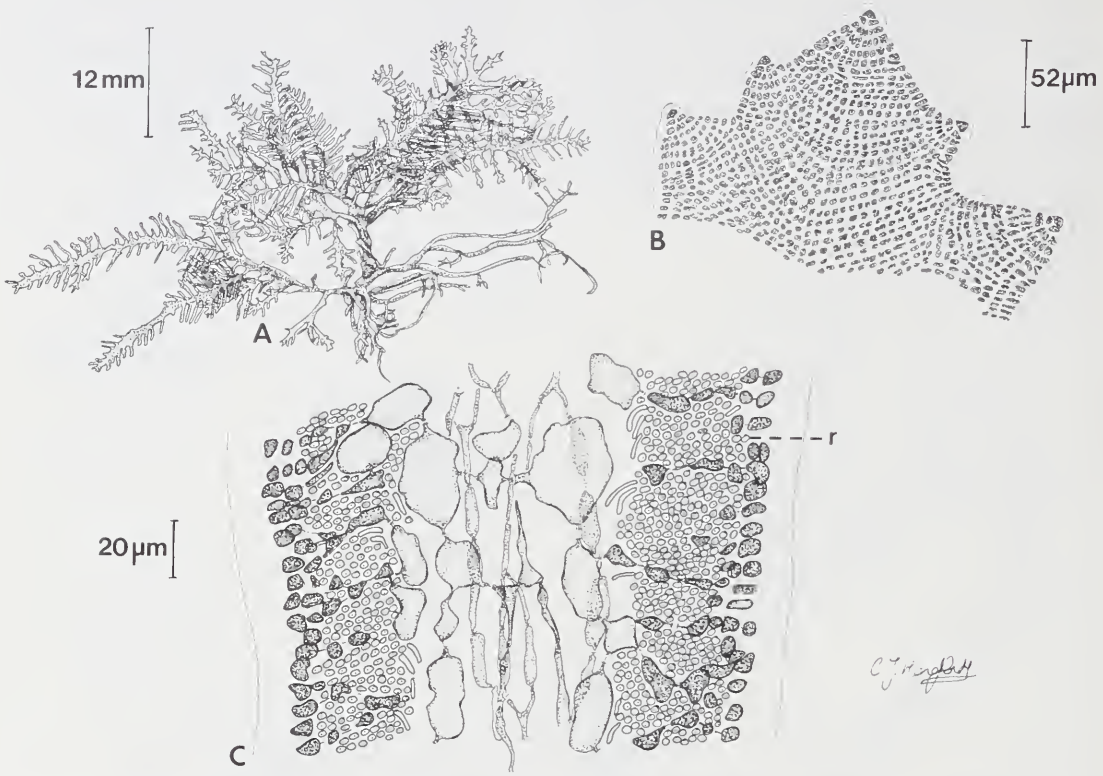

FIGURE 14.—*Ptilophora hildebrandtii*. A, habit of sterile plant; B, branch tip showing arrangement of surface cells; C, longitudinal section of thallus. (Courtesy of the *South African Journal of Botany*.)

NATAL.—Widenham, drift *NU 1525, 3103.* 3130 (Port Edward): Palm Beach, drift, 14-V-1983, *NU 7241, 6276.*

The long mostly unbranched distal branches can be used to separate *P. diversifolia* from its nearest relatives *P. spissa* (Suhr) Kützing, also occurring in Natal, and *P. prolifera* (Harvey) J. Agardh from Western Australia. *P. spissa* is narrower and has pinnately branched distal branches, and *P. prolifera* also has pinnately branched distal regions, but, more importantly, the pinnae have simple elongate determinate laterals that could be classified as elongate serrations. Also, *P. prolifera* does not have a midrib, according to Harvey (1862), whereas both *P. diversifolia* and *P. spissa* have prominent midribs. Thalli of *P. rhodoptera* are similar but commonly have indeterminate adventitious branches from the midrib.

2. **Ptilophora hildebrandtii** *(Hauck) R.E. Norris* in South African Journal of Botany 56: 133 (1990a). Type: Kenya, Mombasa, *Hildebrandt s.n.* (L, lecto.—photo.!). *Lectotype* from Mombasa, Kenya, (collected by J.M. Hildebrandt) in L (figured by Akatsuka (1987)).

Thysanocladia (?) hildebrandtii Hauck: 217 (1886). *Gelidium hildebrandtii* (Hauck) Schmitz: 197 (1894).*Beckerella hildebrandtii* (Hauck) Kylin: 139 (1956).

Icones: Akatsuka: 267, fig. 7, 270, fig. 13 (1987); Norris: 134, figs 1–3 (1990a).

Thalli with rhizomatous holdfasts, erect branches up to 400 mm high, although only a small thallus, one-tenth that size has been found in Natal (Figure 14A); distichously branched up to fourth order. Branches narrow, usually less than 1 mm broad, midrib not visible in branch axes (Figure 14A, B); ultimate determinate laterals lanceolate to somewhat irregular in form. Rhizines abundant in inner cortex, forming bundles between filaments of pigmented cells (Figure 14C); large spheroidal to ellipsoidal cells in one or two rows inside rhizine layer. Central area comprised of elongate cells in filaments. Reproductive stages not found for this species.

Distribution: East African tropical coast, subtidal.

NATAL.—2732 (Ubombo): 5 Mile Reef, Sordwana Bay, *P. Sydenham, diving to 19–22 m, Nat 5285.*

3. **Ptilophora pectinata** *(A. & E.S. Gepp) R.E. Norris* in Botanica Marina 30: 252 (1987h). Type: Australia, New South Wales, Maroubra Bay, *A,H,S, Lucas 9* (BM, holo.).

Pterocladia lucida forma *pectinata* A. & E.S. Gepp: 254 (1906). *Pterocladia pectinata* (A. & E.S. Gepp) Lucas: 408 (1941). *Beckerella pectinata* (A. & E.S. Gepp) Fan & Papenfuss in Fan: 322 (1961).

Gelidium lucasii May: 226 (1944).

Gelidium helenae Dickinson: 565 (1950). *Beckerella helenae* (Dickinson) Fan & Papenfuss in Fan: 322 (1961).

Icones: Lucas: 408, pl. 23, fig. 2 (1931); May: 226–228, figs 1–6; Dickinson: 264, pl. 3 (1950); Fan: 366 (1961); Akatsuka: 268, fig. 8 (1987); Norris: 247, figs 8, 9 (1987h).

Thalli perennial, up to 300 mm tall, growing from a determinate rhizomatous holdfast, rachis narrow (up to

2 mm broad) with interrupted midrib (Figure 15A); lateral branches regularly spaced (every 1.5–2.5 mm) pectinate, simple determinate, flattened, up to 10 × ± 1 mm; often with acuminate tips, sometimes pinnately branched, particularly near distal regions of thallus where they may form longer and perhaps indeterminate laterals; determinate branchlets often missing in proximal parts of thallus leaving dentate margins along thickened axis (Figure 15A). In proximal regions axis also becomes cylindrical with little to no evidence of flattening (Figure 15E). Distinct layers of tissues also evident in sections of this region, central medulla has filaments dispersed in all directions with a tendency to being radially organized, whereas in layer intermediate between medulla and cortex, filaments directed around large cells and often extended in a more tangential plane. Sections of short determinate laterals sometimes have medullary filaments, rhizines and large cells intermixed in medulla with packets of rhizines also delimited by filaments in inner cortex (Figure 15D).

Reproduction: fertile branchlets grow from distal ends of determinate lateral branches, filiform, expanded near tip to bear a single biloculate and biporate cystocarp, usually apiculate (Figure 15B, C), or a tetrasporangial sorus (Figure 15F).

Distribution: New South Wales, Australia, and Richards Bay, Natal.

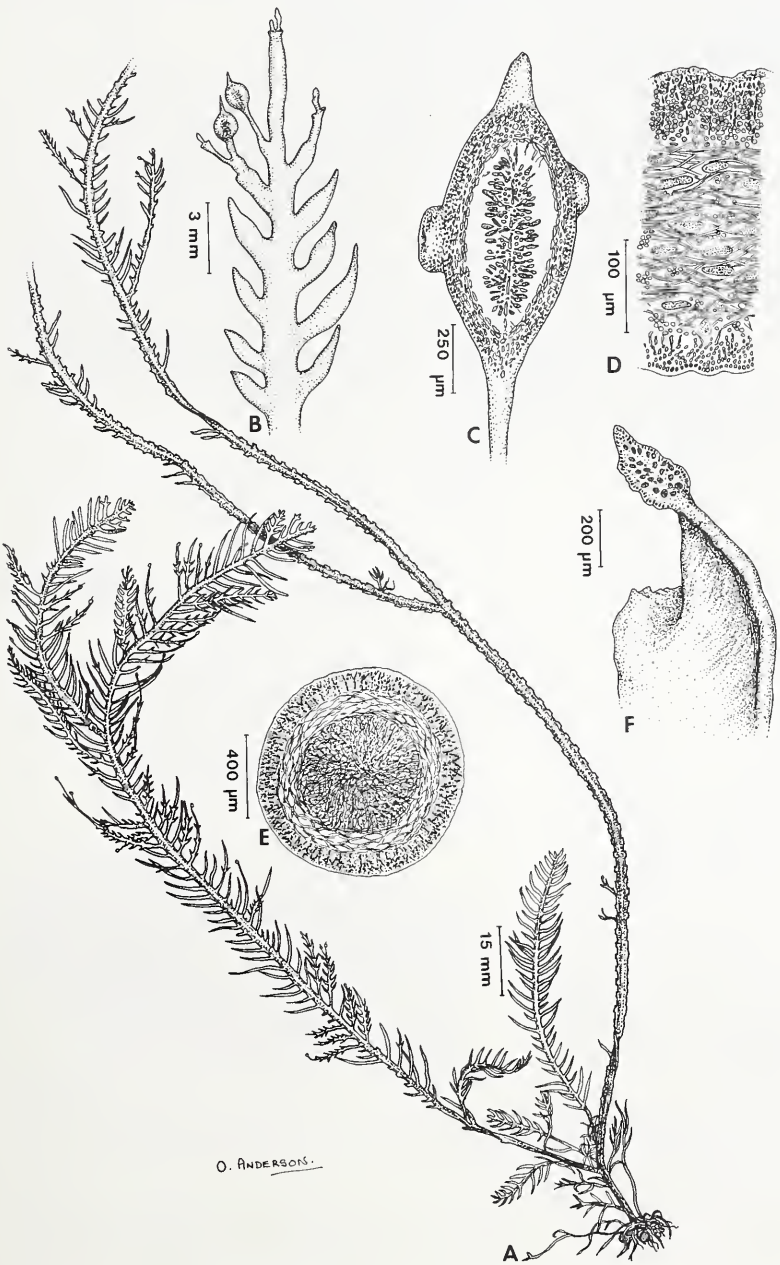

FIGURE 15.—*Ptilophora pectinata*. A, habit of cystocarpic plant; B, enlargement of branch bearing cystocarpic branchlets; C, cross section of a cystocarp; D, cross section of thallus ala; E, cross section of old cylindrical region of thallus; F, tetrasporangial sorus on bladelet proliferation.

FIGURE 16.—*Ptilophora pinnatifida*. A, habit of plant; B, branchlet bearing terminal cystocarps; C, branchlet bearing tetrasporangial sori on marginal bladelets; D, longitudinal section of edge of tetrasporangial sorus; E, cross section of ala margin.

NATAL.—2832 (Mtubatuba): Richards Bay, drift, *Pocock 13241* (GRA); drift, *Pocock 10783; Papenfuss & Scagel I.I.O.E. PR-XXX4a* (NU, NUC).

Formerly known only in eastern Australia, this species is distinctive and easily recognized by its narrow axis in which the midrib may be discontinuous or indistinct. The numerous, simple, pinnately arranged determinate lateral branches are characteristic of this species and *P. rumpii*. The latter species, however, always has much broader alae bordering a distinct midrib that extends most of the thallus length. There seems to be no reliable differences between *P. pectinata* and *P. helenae*.

4. **Ptilophora pinnatifida** *J. Agardh* in Lunds Universitets Årsskrift, Afdelningen för Mathematik och Naturvetenskap 21,8: 79 (1885). Type: South Africa, Cape Province, Algoa Bay, *Em. Holub s.n.* (LD, No. 33300).

Gelidium pinnatifidum (J. Agardh) Schmitz: 194 (1894). *Beckerella pinnatifida* (J. Agardh) Kylin: 139 (1956); Fan: 324 (1961).

Ptilophora beckeri Holmes: 350 (1896). *Beckerella beckeri* (Holmes) Kylin: 139 (1956).

Icones: Fan: 333, 362, 367 (1961); Norris: 248, fig. 9, 249, fig. 10, 250, fig. 11 (1987a); Akatsuka: 270, fig. 11 (1987).

Thallus perennial, up to 300 mm tall, with determinate rhizomatous holdfast and highly branched upright branches (Figure 16A); older specimens with cylindrical to compressed branching axis that becomes alate distally, alate regions up to 10 mm broad with a distinct midrib; determinate lateral branches regularly spaced in alate regions, simple to tridentate or pinnate, all branch tips conical, often with serrations or small branchlets; midribs extend near to branch tips and a branch of midrib extends into some of larger determinate lateral branchlets. Anatomy of alae (Figure 16E) is typical for *Ptilophora* with angular small cells forming a single-layered outer cortex, next layer 1–3 rows of spheroidal cells which enclose a thick layer of rhizoids in packets outlined by filaments of pigmented cells. Medulla filamentous with some areas pseudoparenchymatous; few rhizines present.

Reproduction: all reproductive organs borne on special determinate lateral branchlets that are borne terminally or marginally on serrations. Tetrasporangial branchlets cordate and spatulate (Figure 16C), sori with similar cordate shape inside a broad sterile margin. Rhizines not present or few in fertile branchlets, their absence possibly allowing more rapid release of sporangia. Cystocarps (Figure 16B) usually on terminal determinate branchlets without a distal protuberance of branchlet.

Distribution: southern Natal to eastern Cape Province.

NATAL.—Widenham, drift, *NU 1239*. 3030 (Port Shepstone): Park Rynie, Rocky Bay, drift *NU 3928*. 3130 (Port Edward): Palm Beach, drift, *Nat 1917, NU 8758 & 8759*.

5. **Ptilophora rhodoptera** *R.E. Norris* in Botanica Marina 30: 254 (1987h). Type: Natal, Rocky Bay, Park Rynie, in drift, *Nat 370, NU 9522*.

Icones: Norris: 252, 253 (1987h).

Thallus up to 350 mm tall, comprised of thick cylindrical to compressed proximal axis, 3.5 mm broad, and irregularly proliferous blades emerging from axis and terminating branches (Figure 17A); proliferous blades and distal parts of axes broadly alate, up to 10 mm broad, with conspicuous midrib extending to branch apices, and crenulate to coarsely serrate margins; branches emerge from margins of alae, midrib continuous with main midrib; branch apices broadly rounded, retuse to emarginate and often with bladelet in apical incision. Young alae tissue (Figure 17C) without a central filamentous medulla and rhizines restricted mostly to inner cortex. In older parts of alae as well as in midribs, medulla has filaments of elongate cells mixed with rhizines (cross-section in Figure 17B), a tissue separating the large cells into two layers that now lie in inner cortex, outlined by two layers of small pigmented cortical cells in filaments and packets of rhizines.

Reproduction: only tetrasporophytes known. Small fertile bladelets in irregular positions along margins of alae, cordate and often retuse, entire surface fertile; except for a narrow margin (Figure 17D).

Distribution: known only from the type locality.

This is a very distinctive species recognized by its broad blades with conspicuous midribs extending to the retuse branch tips.

6. **Ptilophora rumpii** *(Dickinson) R.E. Norris* in Botanica Marina 30: 254 (1987). Type: Natal, Richards Bay, *W.G. Rump s.n.*, 1929, (BM, holo.).

Gelidium rumpii Dickinson: 565 (1950). *Beckerella rumpii* (Dickinson) Fan & Papenfuss in Fan: 322 (1961).

Icones: Dickinson: 565, pl. 4 (1950); Norris: 255 (1987h); Akatsuka: 269 (1987).

Thallus up to 360 mm tall, arising from fibrous holdfast, with alae on axis in irregularly arranged sections up to 10 mm broad and with conspicuous midrib (Figure 18A); determinate branchlets distichously arranged on margins of alae at more or less regular intervals up to 1 mm apart, up to 4 × 1 mm, usually simple, with obtuse to apiculate tips. Some determinate lateral branches once pinnately branched but these may be indeterminate branch initials. Alate segments with tapering proximal and distal ends and intervals of axes without alae may be present between segments. Distal parts of branches usually alate in the form typical for the intercalary alate segments, usually a midrib to distal region; branch tips conical, often tridentate. Axis with extensive filamentous medulla (Figure 18B) comprised of irregularly shaped cells intermixed with rhizines; medulla enclosed by layer of large cells followed by layer of rhizines intermixed with filaments of irregular cells, outer cortex with single layer of small cells.

Reproduction: fertile branchlets borne terminally on determinate laterals (Figure 18C, D), tetrasporangiate sori cordate to elongate eilliptical. Cystocarps not observed.

Distribution: known only from several collections at the type locality.

NATAL.—2832 (Mtubatuba): Richards Bay, drift, *Pocock 13242*, (GRA); *Papenfuss & Scagel, I.I.O.E PRXXX-3, 4*, (UC, UBC).

The broad alate sections of the thalli, each having a mostly uniform width and each having a midrib extending

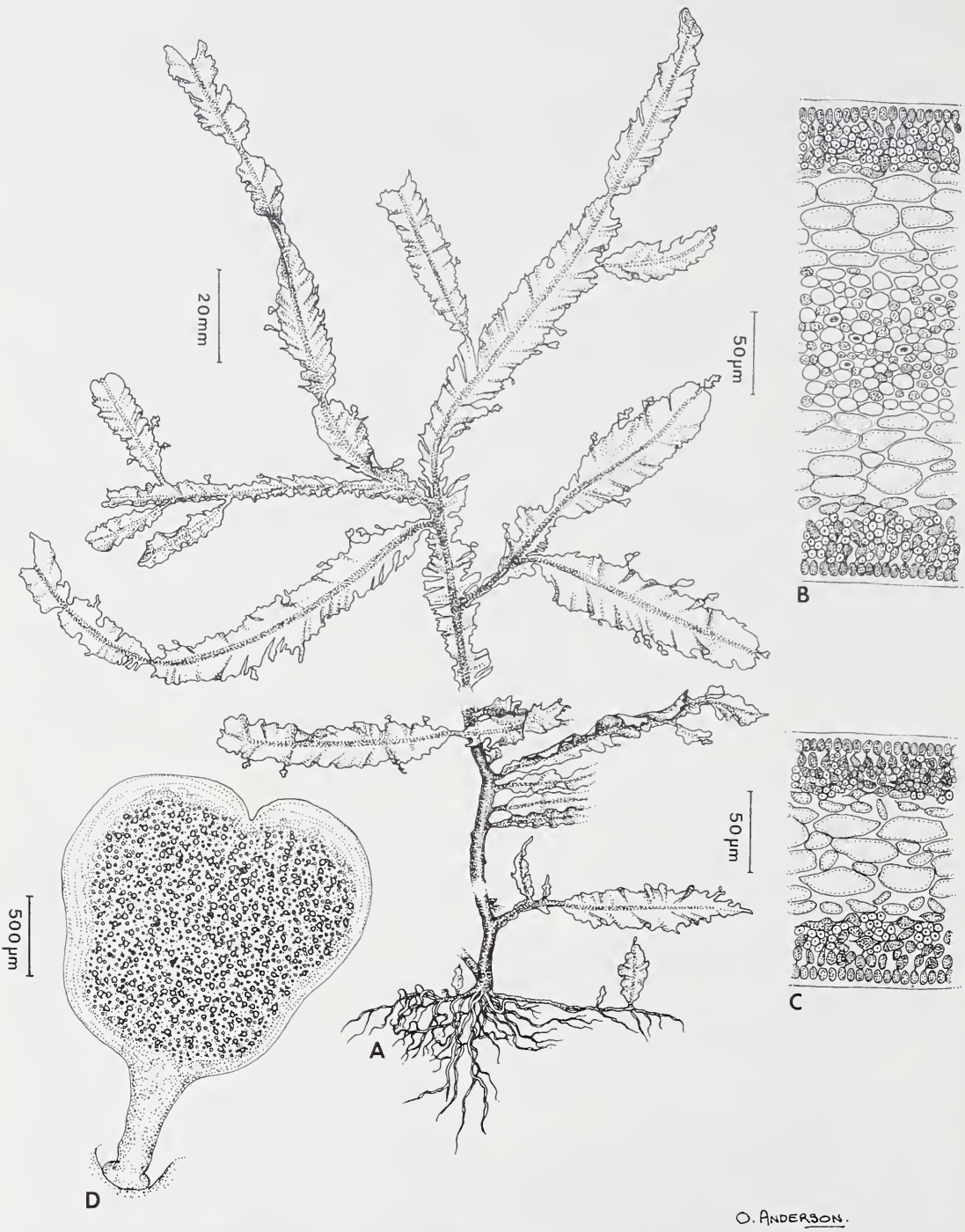

FIGURE 17.—*Ptilophora rhodoptera*. A, habit of plant (parts eliminated at two broken regions of axis); B, cross section of midrib; C, cross section of ala; D, tetrasporangial bladelet from margin of thallus in A. (Courtesy of *Botanica Marina*.)

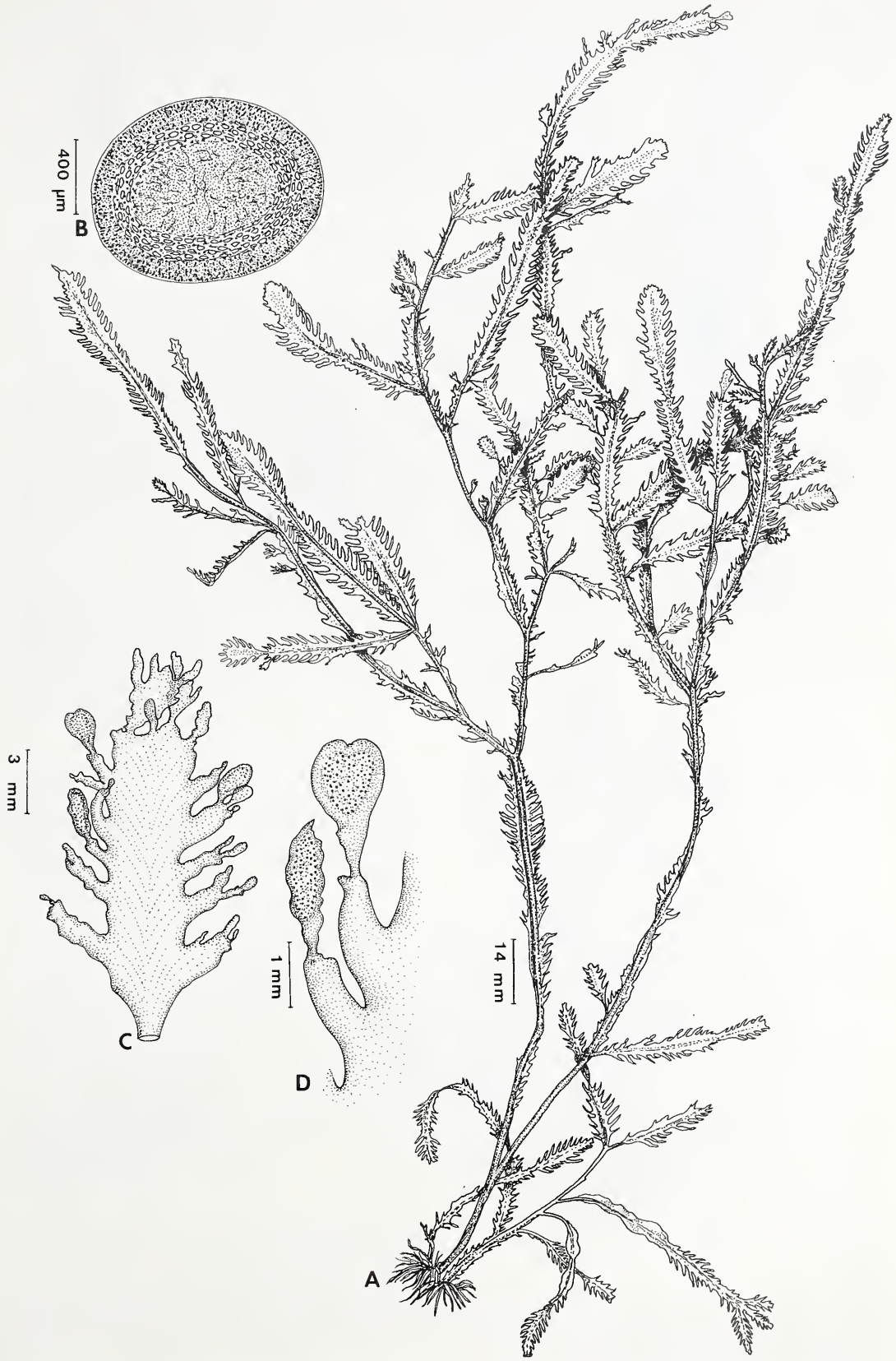

FIGURE 18.—*Ptilophora rumpii*. A, habit of plant; B, cross section of old cylindrical region of axis; C, branch tip bearing tetrasporangial bladelets from plant shown in A; D, enlargement of two tetrasporangial sori.

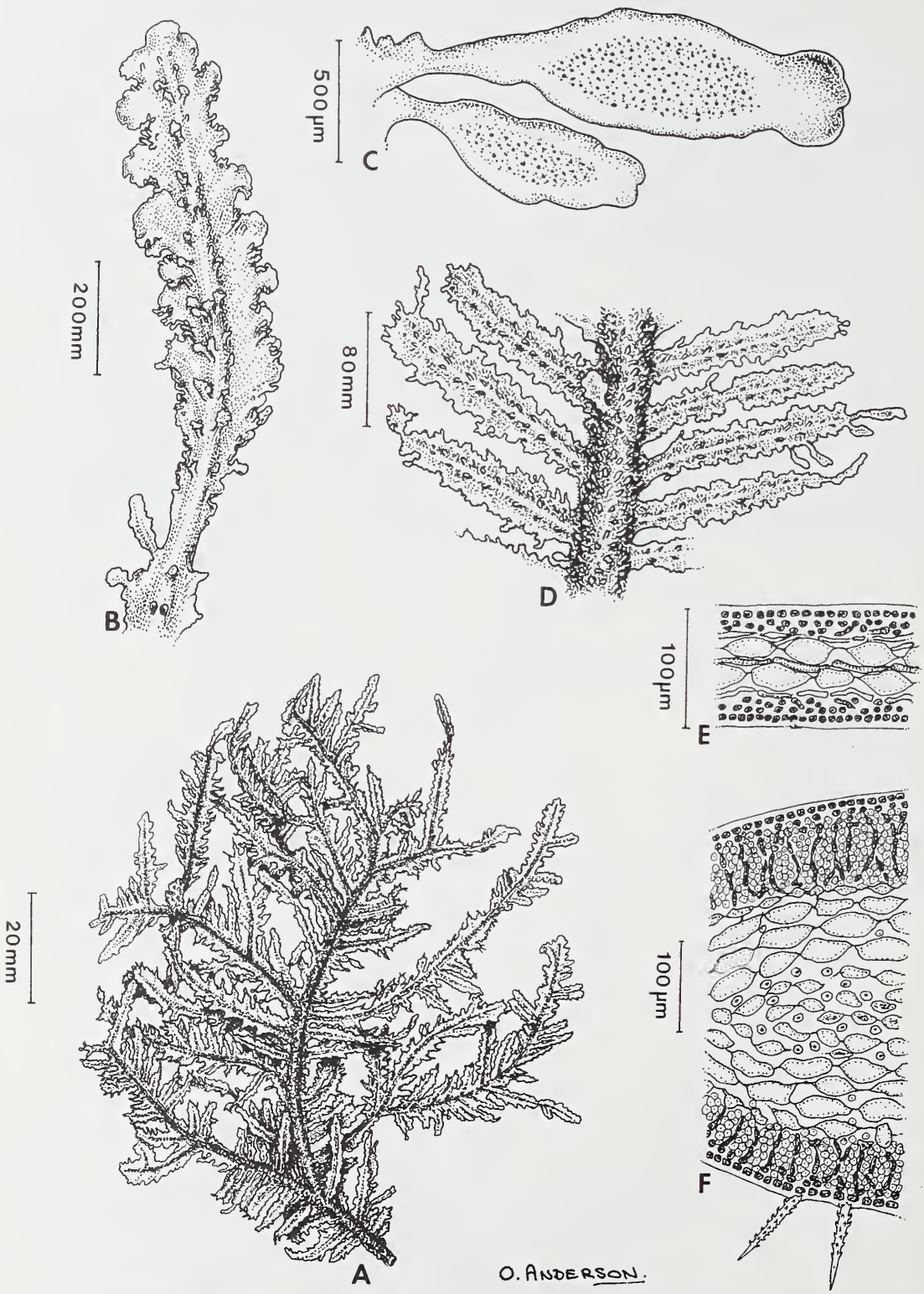

FIGURE 19.—*Ptilophora spissa* (holotype, W). A, entire specimen, a tetrasporophyte; B, enlarged branch with ala showing sparse surface proliferations; C, two fertile branchlets bearing tetrasporangial sori; D, part of plant axis with distichous branchlets, thick proliferations on axis where sponge infection is strong; E, longitudinal section of ala; F, cross section of thallus axis where sponge covering occurs showing two spicules on lower side.(Courtesy of *Botanica Marina*.)

through it, are distinctive characters for this species. In addition, the mostly unbranched regularly spaced determinate lateral branchlets are characteristic for this species and the much narrower *P. pectinata*.

7. **Ptilophora spissa** *(Suhr) Kützing* in Botanische Zeitung 5: 25 (1847); Papenfuss: 214 (1940). Type: Natal, 'Omsamculo' (between the Umzimkulu and Umkomaas Rivers according to Papenfuss, 1940), *Drège s.n.* [W. lecto. by Fan: 356 (1961)].

Phyllophora spissa Suhr: 262 (1840).

Icones: Kützing: 19, pl. 45, figs e–g (1869); Fan: 356 (1961); Norris: 257 (1987h).

Thallus up to ± 50 mm long, branches with prominent midrib, covered with small proliferous outgrowths, especially in proximal regions (Figure 19A, B, D); margins of thalli strongly crenulate and thallus surfaces often covered by thin layer of sponge. Thallus branches pinnately arranged, mostly in an irregular manner, sometimes densely pinnate but in other regions without pinnae. Pinnae usually not secondarily branched except when they become indeterminate. Alae thin (Figure 19E) and with large cells in medulla intermixed with a few narrow-celled filaments. A few rhizines may be present in inner cortex. Midrib and thicker regions of blades (Figure 19F) have rhizines in centre of medulla mixed with small-celled filaments; inner cortex of these regions have a thick layer of rhizines intermixed with pigmented filaments.

Reproduction: tetrasporangial sori often lanceolate with wide sterile margin, borne on small marginal bladelets (Figure 19D), which are elliptical in outline (Figure 19C).

Distribution: known only from the type collection.

Unfortunately this, the type species of *Ptilophora*, is the least known of all the species in the genus and I have examined only the type specimen, no fresh specimens having been found. The information presented here, therefore, is from my studies on the type specimen which has a few fertile branchlets bearing tetrasporangia.

Family Gelidiellaceae Fan

Thalli with both prostrate and erect branching systems, soft to firmly cartilaginous, cylindrical to compressed; erect branches usually determinate in growth, with single apical cell forming a subapical cell that has longitudinal divisions in 2 directions; subsequent cells in axial filaments with divisions at right angles in an alternating series forming decussate pattern (Sreenivasa Rao 1971); thallus with unbranched, irregularly branched or with mostly distichous, sometimes decussate, arrangement of branches. Medulla comprised of elongate parenchymatous cells, cortex with small ellipsoid to spheroid cells, rhizines not present in members of this family.

Reproduction: tetrasporangia formed in stichidial branch apices on erect system, borne in distal positions, in place of outer cortical cells, a single one terminating many of tertiary and higher orders of filaments in fertile region of branch. In other species stichidia compressed, tetrasporangia borne on short tertiary determinate filaments along axis of secondary branch resulting in subsequent chevron rows of sporangia in fertile region.

Cystocarps of an unknown species of *Gelidiella* were described by Sreenivasa Rao & Trivedi (1986), the only report of gametophytic plants for the Gelidiallales. Uniloculate urceolate cystocarps terminate branches, the floor of which is lined by nutrient filaments that directly produce gonimoblast. Male plants were not described.

Separated as a family in 1961 by Fan, the Gelidiellaceae was considered to be indistinguishable from the Gelidiaceae by Maggs & Guiry (1987). Re-assessing the characters used by Fan, with emphasis on the absence of rhizines, and adding the decussate branching pattern as important in defining the Gelidiellaceae, I prefer to continue recognition of this family. It may be that all members of the Gelidiellaceae have only indeterminate prostrate branches, the erect ones always being determinate. Species of the Gelidiaceae, some species of which may also have this growth form, more often have determinate prostrate branches, forming a holdfast system, and indeterminate upright branches originating from severel places in the holdfast system. These characters were considered particularly important in proposing an evolutionary scheme for the Gelidiales (Norris 1992a) in which the Gelidiellaceae were tentatively assigned a more primitive status.

GELIDIELLA

Gelidiella *Feldmann & Hamel* in Revue Générale de Botanique 46: 529 (1934). Type species: *G. acerosa* (Forssk.) Feldmann & Hamel.

Echinocaulon Kützing: 405 (1843), nom. illeg., non *Echinocaulon* Spach (1841). Type: *E. spinellum* Kützing: 406 (1843) [= *Gelidiella acerosa* (Forssk.) Feldmann & Hamel].

Acrocarpus Kützing: 405 (1843), nom. illeg., non *Acrocarpus* Wight (1839). Lectotype: *Acrocarpus lubricus* Kützing: 406 (1843) [= *Gelidiella lubrica* (Kützing) Feldmann & Hamel].

For further description and discussion see Norris (1992a).

Thalli with indeterminate prostrate branches, forming rhizoids directly from ventral cells or rhizoids developed in groups forming peg-like holdfasts; upright determinate branches develop in irregular positions on dorsal side of prostrate branches; all branches cylindrical to compressed, terminated by single apical cell that divides to form a subapical cell from which two periaxial cells are derived. Periaxial cells in decussate arrangement on subsequent axial cells, initiate cortex and medulla from primary filaments and their derivatives. Branching of thallus occurs only by adventitious transformation of cortical cell into an actively dividing apical cell (Sreenivasa Rao 1971). Cells in thallus centre become enlarged and elongate but cells in inner cortex smaller and spheroid to ovoid. Outer cortical cells are smallest and form a compact pigmented tissue that, covered by a cuticle, envelops thallus. Secondary pit connections occur between cells in internal tissue.

Reproduction is as discussed in the family description.

Although *Gelidiella acerosa*, the only species previously reported in this region, was excluded from the South

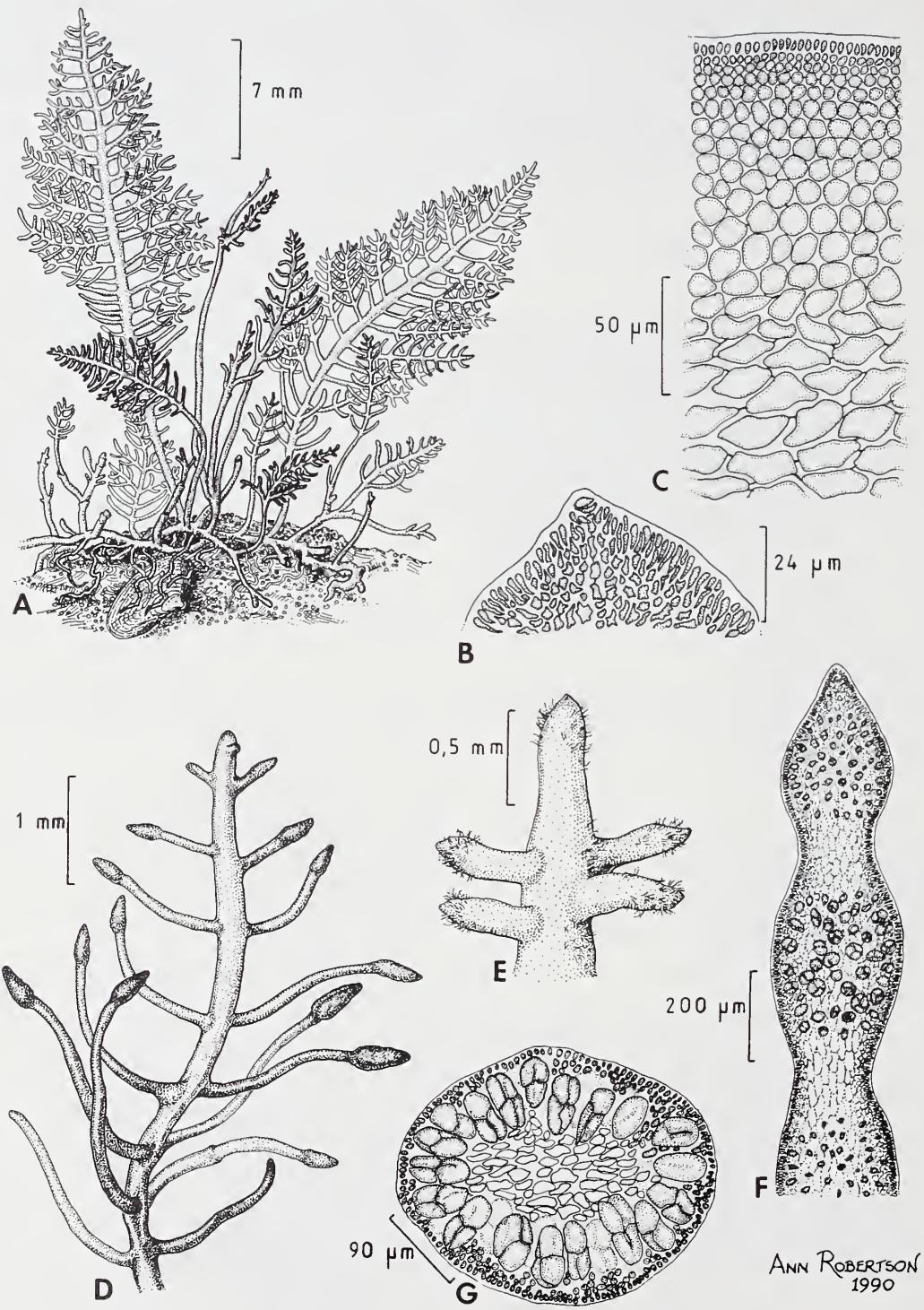

FIGURE 20.—*Gelidiella acerosa*. A, habit of thallus growing on rock and small mussel shell; B, enlargement of branch tip showing apical cell; C, partial cross section of thallus; D, branch bearing fertile tetrasporangial sori on tips of branchlets; E, branch tip showing hairs from cortical cells near apices of branchlets; F, tetrasporangial branchlet showing pulses of fertility resulting in diameter increase in branchlet; G, cross section of tetrasporangial fertile area.

African flora by Papenfuss (1952). Seagrief (1980) illustrated an unidentified species that he assigned to this genus, a species that is probably *G. acerosa*. Our collections in northern Natal show that *G. acerosa* is relatively common in intertidal situations, and that two other species also occur in Natal.

Key to Natal species of *Gelidiella*

1a Prostrate system attached by rhizoid outgrowths from most ventral cells; upright branches mostly unbranched; 4 tetrasporangia in a fertile segment ..... 2. *G. antipai*

1b Prostrate system attached by groups of rhizoidal outgrowths forming peg-like holdfasts; upright system branched; more than 4 tetrasporangia in a fertile segment:

2a Branching of upright system irregular; tetrasporangial stichidia terminating long branches or sometimes on special short laterals ..... 3. *G. lubrica*

2b Upright system with short determinate lateral branchlets, often pinnate; branchlets commonly distichously arranged; tetrasporangial stichidia terminating lateral branchlets 1. *G. acerosa*

1. **Gelidiella acerosa** *(Forssk.) Feldmann & Hamel* in Revue Générale de Botanique 46: 533 (1934). Type: from Mokha, Yemen.

Fucus acerosus Forssk.: 190 (1775).

Fucus rigidus Vahl: 46 (1802).

Sphaerococcus rigidus C. Agardh: 285 (1822). *Gelidium rigidum* (C. Agardh) Greville: lvii (1830). *Gelidiopsis rigida* (C. Agardh) Weber-Van Bosse: 104 (1904).

Fucus spiniformis Lamouroux: 77 (1805). *Gelidium spiniforme* (Lamouroux) Lamouroux: 129 (1813).

Thalli with branch systems both prostrate and erect, up to 90 mm tall; prostrate system branching irregularly forming upright mostly determinate and fertile branches from dorsal side of prostrate system, and special anchoring branches that form lateral peg-like haptera or terminal clusters of multicellular rhizoids (Figure 20A) (Sreenivasa Rao 1971); upright branches, up to 1 mm broad, often have pinnately arranged branchlets that may branch a second time. Some branchlets may be irregularly placed or decussate, not following a distichous pattern, sometimes decumbent and attached to other branches or substratum. Hairs often present on cells near distal end of branchlets (Figure 20E) and have a structure as described for this species by Akatsuka (1970, 1982). All branches cylindrical to somewhat complanate. Single large apical cell terminates branches (Figure 20B) and divides to form an axial filament, each cell of which may have two branches (Sreenivasa Rao 1971; Norris 1992a), decussately arranged on subsequent axial cells. Outer cortical cells, 3–4 layers, small ovoid to ellipsoidal (Figure 20C), inner cells gradually increasing in size to form large and irregularly-shaped cells in medulla (up to 35 μm in diameter). Secondary pit connections are common, especially between larger interior cells (Sreenivasa Rao 1971) where, because of the thin-walled cells, pit connections usually do not occur on attenuated protoplasmic extensions as in most other floridean algae.

Reproduction: only tetrasporophytes are known for this species. Distal ends of lateral branchlets swollen (Figure 20D) and tetrasporangia terminate lateral branches of the third or fourth order, enclosed by small filaments of outer cortical cells (Figure 20G) (Sreenivasa Rao 1971). Growth of some branches show pulses of fertility, swollen fertile areas alternating with sterile tissue (Figure 20F). Tetrasporangia mostly cruciately divided with a few showing a tetrahedral configuration (Sreenivasa Rao 1971), cytokinesis probably occurring after meiosis is complete because no two-celled stages have been observed.

Distribution: in most tropical intertidal habitats.

NATAL.—2732 (Ubombo): Botelier Point, 27°01′S, 32°52′E, *Balkwill & Emanuel Nat 5565* (SAM 100443); Black Rock, 27°08′S, 32°50′E, *Olivieri Nat 5220*, (SAM 100442); Sordwana Bay, 27°32′S, 32°40′E, *R.E. Norris Nat 6265* (SAM 102038, 102084, 102197, 102198).

2. **Gelidiella antipai** *Celan* in Académie Roumaine, Bulletin de la Section Scientifique 19: 3 (1938). Type: Cape Kaliakra on the Bulgarian coast of the Black Sea.

Gelidiella stichidiospora Dawson: 84 (1953).

Gelidiella adnata Dawson: 422 (1954); Santelices: 63 (1977).

Thalli often forming a turf, prostrate branching system indeterminate, erect system mostly determinate (Figure 21A); erect branches are up to 2 mm high, usually less than 100 μm in diameter and cylindrical to compressed. Ventral cells on prostrate branches develop unicellular rhizoids that attach to substratum (Figure 21B), some long upright branches stoloniferous and attaching by similar rhizoids. All branches with a single apical cell dividing transversely, subsequent filaments decussately arranged on axis (Figure 21D, E). Cortical cells in 1–3 layers, in young regions with long axis arranged transversely on branch. Medulla with elongate cylindrical cells in 5 or 6 transverse rows. Tetrasporangia borne in stichidia terminating upright branches (Figure 21A, C), stichidial diameter approximately twice that of bearing branch. Sporangia 25–35 μm in diameter, cruciately to tetrahedrally divided and 4 borne on each segment of stichidium. Filaments of small cortical cells occupy spaces between tetrasporangia.

Distribution: apparently widespread in tropical, subtropical and warm temperate seas throughout the world.

NATAL.—2732 (Ubombo): found only once, Leadsman Shoal, St Lucia, 27°52′30″S, 32°36′E, *M. Bower* by diving to 10 m, *Nat 2392*.

Identification of small species of *Gelidiella* is difficult because of the uncertainty of character stability, and also the need for verification of species through examination of type specimens. Two characters seem to be important in identifying at least groups of species. 1, the formation of single-celled rhizoids on ventral cells of the prostrate branch contrasted with rhizoids that may be multicellular and are accumulated into peg-like holdfasts; and 2, only 4 tetrasporangia in each fertile segment of the stichidium contrasted with more than 4 tetrasporangia in each segment. *Gelidiella antipai, G. stichidiospora* and *G. adnata* produce 4 sporangia in each stichidial segment and also have rhizoidal cells produced by most ventral cells of prostrate branches. In my estimation there seems to be little reason for maintaining them as separate species. Schnetter & Bula Meyer (1982) recorded a species that does not combine the two characters identifying *G. antipai*, rhizoids on most ventral cells of the prostrate system and 4 sporangia per stichidial segment. In the species they attribute to *G. adnata*, here considered to be a synonym of *G. antipai*, the ventral side of prostrate branches has what appear to be rhizoidal outgrowths on ventral cells occurring in patches on the prostrate branches,

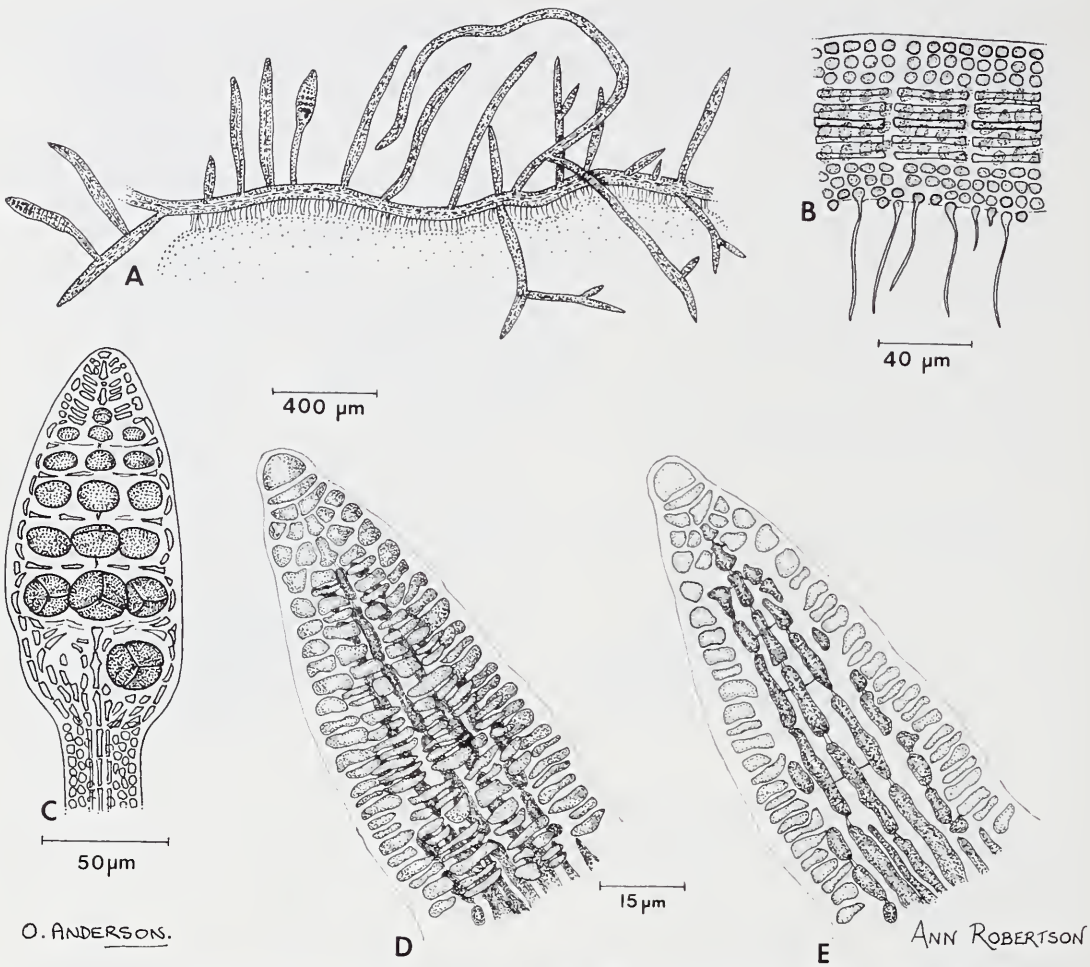

FIGURE 21.—*Gelidiella antipai*. A, habit of plant, note rhizoids on ventral surface of prostrate branch and erect branches arising from dorsal surface; B, part of prostrate branch showing unicellular rhizoids growing from cortical cells; C, erect branch tip bearing a stichidium, note that four tetrasporangia occur in each whorl; D, branch tip showing surface cells; E, branch tip in optical section showing medullary cells.

and many more than 4 tetrasporangia are illustrated in each segment of the stichidium of this species. These characters do not comply with those attributed to *G. adnata* by Dawson, who clearly stated that only four tetrasporangia occur in each stichidial segment.

Small species of *Gelidiella* (less than 20 mm) with peglike holdfasts and with more than 4 tetrasporangia in each stichidial segment may form a more complex species assemblage. Until these various species can be subjected to more rigorous testing of their characters through methods of culture, etc., I prefer to recognize them as a single species and am identifying them with the name which is probably the oldest, *G. lubrica* (Kützing) Feldmann & Hamel.

3. **Gelidiella lubrica** *(Kützing) Feldmann & Hamel* in Revue Générale de Botanique 46: 535 (1934). Type: Naples, Mediterranean, *Kützing s.n.* (L?).

Acrocarpus lubricus Kützing: 405 (1843).

Thalli with prostrate and upright branching systems forming a turf (Figure 22A, B); upright branches up to 150 mm tall, 200 µm broad, often becoming stoloniferous; irregular and sparse, often compressed, especially in distal regions; prostrate branches attached by peg-like clusters of rhizoids formed at irregular intervals on ventral side. Outer cortical cells small, ellipsoidal to spheroidal, in 3–6 layers (Figure 22E); medullary cells about ten times larger, forming central pseudoparenchymatous tissue.

Reproduction: tetrasporangial stichidia elliptical, terminal on branches or sometimes on short lateral branchlets (Figure 22C), about twice as broad as vegetative branches, bearing sporangia in irregular rows of more than four spores (Figure 22D). The apical cell sometimes loses its identity in mature stichidia.

Distribution: tropical to subtropical shores of most seas.

NATAL.—2732 (Ubombo): Black Rock, 27°08′S, 32°50′E, *P. Sydenham Nat 2891* by diving to 4 m; Sordwana Bay, 27°32′S, 32°40′E, *R.E. Norris Nat 6385* intertidal, *SAM 102153*. 3030 (Port Shepstone): Park Rynie, Rocky Bay, 30°20′S, 30°43′E, *R.N. Pienaar Nat 2107* intertidal, *SAM 100452*.

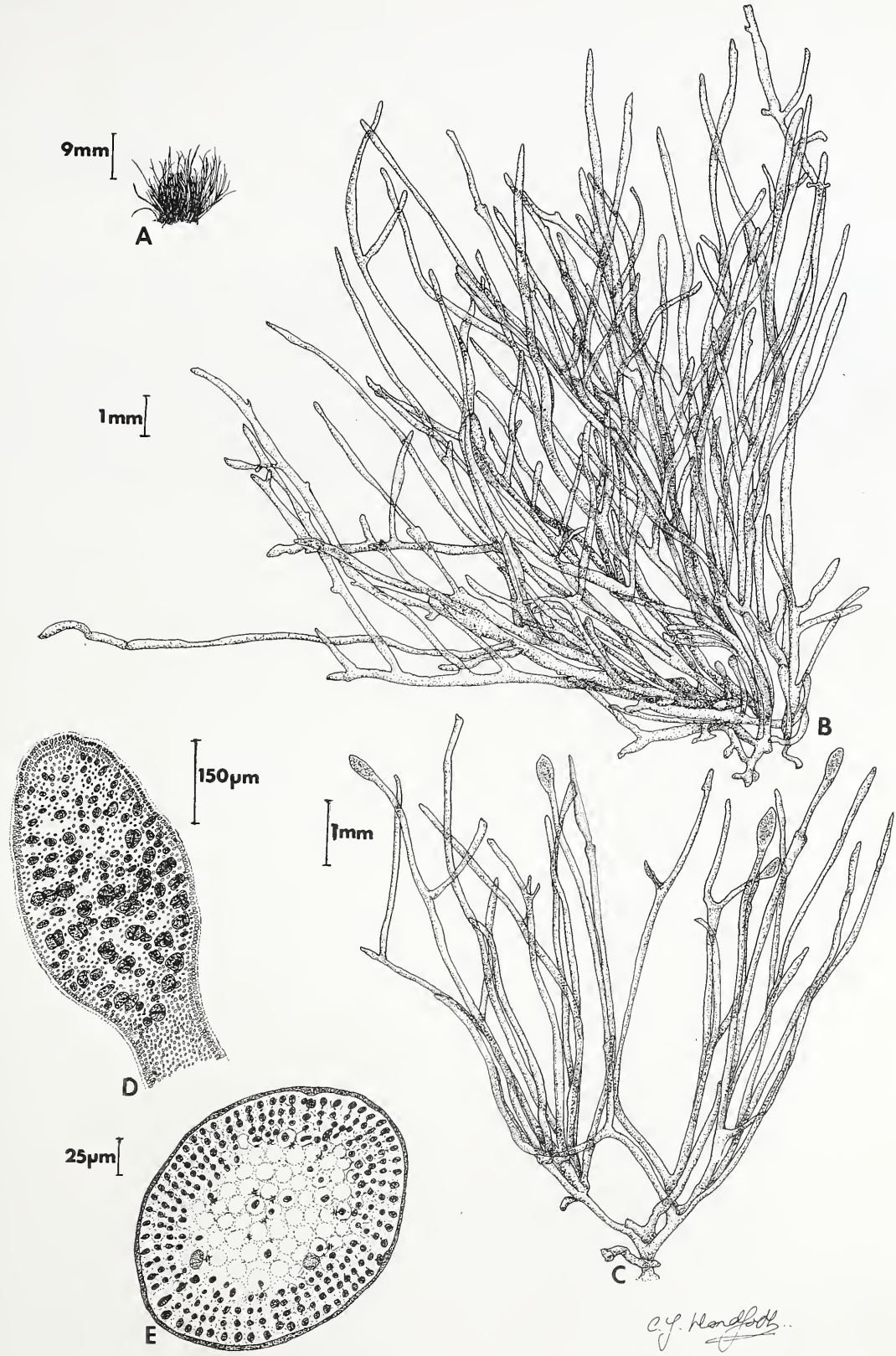

FIGURE 22.—*Gelidiella lubrica*. A, piece of turf formed by this species close to life size; B, enlarged part of thallus; C, thallus bearing terminal tetrasporangial sori; D, enlarged tetrasporangial sorus; E, cross section of branch.

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